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Mammals of the Black Hills of South Dakota and Wyoming

By

Ronald W. Turner

UNIVERSITY OF KANSAS
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April 3, 1974

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University of Kansas
Museum of Natural History

Miscellaneous Publication No. 60
April 3, 1974

Mammals of the Black Hills of South Dakota and Wyoming

By

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A dissertation submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy, The University of Kansas, 1971.

University of Kansas
Lawrence
1974

University of Kansas Publications, Museum of Natural History

Editor: Linda Trueb
Managing Editor: William E. Duellman

Miscellaneous Publication No. 60
pp. 1-178; 14 figures
Published April 3, 1974

Museum of Natural History
University of Kansas
Lawrence, Kansas 66045
U.S.A.

Printed by
University of Kansas Printing Service
Lawrence, Kansas

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INTRODUCTION

The Black Hills have been described as a mountainous island surrounded by a sea of grass. The mesic climate, coniferous forests, rugged and dissected topography, and diversity of geological structures and edaphic features in the Black Hills contrast sharply with the adjacent Northern Great Plains, which are characterized by semi-arid to arid grasslands and gently rolling topography. In some areas, general zones of transition tend to compromise the distinctiveness of these two physiographic entities. In spite of the northern and montane affinities of the Black Hills, the indigenous mammalian fauna is heterogeneous in origin. A definitive biogeographical analysis of the mammalian fauna has not been attempted previously.

The principal purposes of this report are: 1) to delimit and describe the mammalian fauna of the Black Hills of South Dakota and Wyoming (43°10′-44°50′ N lat.; 103°20′-104°50′ W long.) as a natural zoogeographic unit; 2) to describe the autecology and distributional patterns of each mammalian species in the Hills; 3) to discuss the geographic variation and inferred speciation of these mammals; and 4) to analyze and interpret the probable biogeographic affinities of various species in light of proposed changes in late Pleistocene and Holocene environments. Thus, this study represents a synthesis of systematic, zoogeographic, ecologic, and historic factors and their bearing on the contemporary mammalian fauna of the Black Hills.

The Recent Black Hills mammalian fauna comprises 62 species in 44 genera and six orders. Three of the species have been extirpated by man and subsequently reintroduced to the Black Hills from other areas. Four other species (indicated by an asterisk in the Contents) are adventives; of these, two were introduced from North America and two from outside North America. Also included in the accounts are 25 species whose occurrence in the Black Hills is questionable or undocumented at present.

ACKNOWLEDGMENTS

Many persons have contributed directly or indirectly to the completion of this paper. I am particularly grateful to the following persons for the loan of specimens, for information concerning specimens, or for permission to examine specimens: S. Anderson, K. F. Koopman, and R. G. Van Gelder, American Museum of Natural History; J. C. Moore, Field Museum of Natural History; R. R. Mansfield, Minnilusa Historical Museum; W. H. Burt and E. T. Hooper, Museum of Zoology, University of Michigan; J. D. Druecker and J. S. Findley, Museum of Southwestern Biology, University of New Mexico; R. A. Martin, Department of Biology, South Dakota School of Mines and Technology; D. W. Block, E. J. Hugghins, and R. J. Walstrom, Department of Entomology and Zoology, South Dakota State University; B. Harrell, Department of Biology, University of South Dakota; C. O. Handley, Jr., D. A. Schlitter, and H. W. Setzer, U. S. National Museum; R. H. Manville and J. Paradiso, U. S. Fish and Wildlife Service (Biological Surveys Collection); C. A. McLaughlin, Department of Zoology, University of Wyoming; and N. R. Whitney, Rapid City, South Dakota. I am indebted to Park Superintendent W. D. Hotchkiss and Chief Park Naturalist G. B. Robinson of Wind Cave National Park for providing physical facilities and access to records on file at the Park. I wish to extend special recognition to J. A. King, Department of Zoology, Michigan State University, for making available his unpublished field notes and

supplementary observations which greatly enhanced my study. I also wish to thank R. Barbour and W. H. Davis, Department of Zoology, University of Kentucky, for assistance in the field in the summer of 1968.

Some 46 persons associated with the Museum of Natural History of The University of Kansas participated in field work in the Black Hills from 1947 to 1967. I want especially to recognize S. Anderson, R. H. Baker, E. L. Cockrum, E. R. Hall, J. K. Jones, Jr., C. A. Long, and H. W. Setzer, whose expeditions resulted in specimens and comprehensive field notes used in preparation of this report.

For identification of ectoparasites, I am indebted to K. C. Emerson, U. S. Army; E. Garret, Bishop Museum, Honolulu; C. E. Hopla, Department of Zoology, University of Oklahoma; G. M. Kohls, Rocky Mountain Laboratory, Hamilton, Montana; R. B. Loomis, Department of Biology, Long Beach (California) State College; B. McDaniel, Department of Entomology and Zoology, South Dakota State University, Brookings, South Dakota; B. V. Peterson, Canada Department of Agriculture, Ottawa; R. D. Price, Department of Entomology, Fish, and Wildlife, University of Minnesota; the late R. L. Usinger, Department of Entomology, University of California (Berkeley); N. Wilson, Department of Biology, University of Northern Iowa, Cedar Falls; and W. J. Wrenn, Department of Entomology, The University of Kansas.

The cooperation of the South Dakota Department of Game, Fish and Parks is fully appreciated. Scientific collecting permits were kindly issued by V. Johnson and J. W. Sprague. Chief of the Division of Game Management, J. Popowski, and State Game Biologists, L. Petersen and A. H. Richardson, contributed significant information concerning the artiodactyls and carnivores in the Black Hills region. State Game Wardens R. Butterfield, O. Meadows, C. Webster, and E. L. Woods also donated specimens and information pertaining to the larger fur-bearers in their respective districts. I am especially grateful to Assistant Chief Ranger J. F. Devenport, Wind Cave National Park, for contributing his firsthand knowledge of wildlife within the Park and adjacent regions. The advice of A. C. Meland, Soils and Water Conservation Service, concerning the edaphic characteristics of the Black Hills region is appreciated. A number of personnel in the U. S. Forest Service, Black Hills National Forest, advanced my study in innumerable ways. Among these I would mention especially I. Case, W. D. Cloud, F. Fichtner, A. W. Jones, D. Kocer, G. Roby, K. C. Scholz, and J. C. Windsor. I am indebted to all those listed above and others unnamed, who gave generously of their time and efforts in my behalf.

The National Science Foundation (through fellowships to student participants for field work in June and July of 1965 and 1967 under Grant GE-7739), The Museum of Natural History, the Department of Zoology, and the Committee of Systematics and Evolutionary Biology (NSF Grant GB-4446X) at The University of Kansas, and a Watkins Museum of Natural History Grant, all helped to defray cost of field operations. A computer grant from the Department of Systematics and Ecology enhanced statistical analysis of the data.

I am grateful to other friends and associates, especially Elmer C. Birney, John B. Bowles, Hugh H. Genoways, and Carleton J. Phillips, who have given of their time and criticisms, and I am obliged to Barry L. Siler for preparing the illustrations. To my wife, Barbara M. Turner, I give special recognition for her patience and perseverance during the final phases of the project and for typing the first draft of the manuscript. Similar recognition is given to Mary H. Michener for reading the final proof.

I am indebted to Robert S. Hoffmann and Ronald McGregor who supported my investigation through encouragement and contribution of crucial counsel. In addition, Wakefield Dort, Jr., and A. W.

Kuchler read and criticised portions of the manuscript. I extend my thanks to Howard J. Stains, Southern Illinois University, who first instilled in me an interest in zoology, and through his teaching and personal example gave great impetus to my formal education.

Especially instrumental in the formation and completion of my study was J. Knox Jones, Jr., who gave continued guidance throughout the duration of the project, devoted many arduous hours to counseling, assisted in field problems, and aided in preparation of the completed manuscript. His unselfish assistance is acknowledged with sincere gratitude. Professor Jones proved himself to be capable of considerable patience, the depths of which only I can truly appreciate.

HISTORICAL RESUMÉ

Little is known about prehistoric man in the Black Hills area. Archeological findings from several sites indicate that early inhabitants of the area (7000-9000 BP) were bison hunters organized socially into small hunting bands, each composed of several cooperating families (Black Hills Area Resource Study, 1967: 21). Several Indian tribes (in chronological sequence: the Poncas, Kiowas, Crow, and Cheyennes) lived near the Hills at different times. When white men first came, the region was in the possession of the Teton-Dakotas, more commonly called the Sioux. However, the Sioux were immigrants, drifting west from the Great Lakes country and displacing the Cheyennes as late as the mid-eighteenth century.

The Black Hills region is rich in history, much of which has been recorded in accounts of the pioneers that settled there. I have not attempted to consult the vast historical literature, but rather have restricted myself to accounts of the various scientific and military explorations of the study area. Results of these expeditions are recorded in several Reports of the Secretary of War in the Executive Documents of Congress. Additional information can be obtained from the collections and publications of the South Dakota State Historical Society, Pierre, South Dakota 57501.

Francois and Louis-Joseph Verendrye, two French explorers, entered the Black Hills in early February of 1743; they were probably the first white men to penetrate the region. Although Meriwether Lewis and William Clark did not enter the Hills proper, a French trader, Valle, encountered the explorers near the mouth of the Cheyenne River and told them of the "Black Mountains" to the west. Having received similar reports while camped at the mouth of the Bad River in 1833, Prince Maximillian termed this pine-clad range the "Black Hills" (Thwaites, 1906). He also included the Killdeer Mountains and Little Missouri River Badlands of North Dakota under this designation (Bailey, 1927:25). Both Hunt's American Fur Company Astoria Expedition (1811) and Jedediah Smith's expedition of 15 fur traders (1823), passed through parts of the Black Hills. Additionally, there was a number of other traders and trappers who traversed the Hills during the first half of the nineteenth century, but these men left little record of their passing. Fur trading posts were established near the mouth of the Belle Fourche River and on the White River, near the mouth of Wounded Knee Creek, as early as 1828.

Scientific exploration of the region began in 1852, when Dr. John Evans mapped the Badlands and the eastern foothills under the auspices of the David Dale Owens Geological Survey. In March 1853, Congress appropriated funds for a survey of various proposed routes, along which a railroad might be constructed from the Mississippi River to the Pacific Ocean. Survey parties were organized by the War Department, and supplies for collection of natural history objects were provided by the Smithsonian Institution. The first known specimens of mammals from the Hills were

taken by these expeditions. Topographical and geographical knowledge of the country along the White and Bad rivers was incremented in 1855 with the military expedition headed by General William S. Harney, and including topographical engineer Lieutenant G. K. Warren, and geologist Dr. F. V. Hayden. This party passed along the southern periphery of the Black Hills from Fort Laramie enroute to Fort Pierre (Warren, 1856). Two years later, Hayden again accompanied Lt. Warren to the region, recording observations on 44 kinds of mammals (Hayden, 1859). Entering from the south by way of Stockade Beaver Creek (Weston County), they traveled along the western edge of the Hills to Inyan Kara Mountain, Crook County, Wyoming (Fig. 2). Here they were turned back by threatening bands of Hunkpapa and Miniconjou Sioux; they traveled southeastward to the vicinity of Rapid City, then north to Sturgis and Bear Butte and returned to Missouri via the Niobrara River (Warren, 1856; 1859; Hayden, 1856; 1859). Hayden (1862: 138-151) summarized his observations on the natural history of the Upper Missouri based on excursions from 1854 to 1862 commenting on 59 kinds of mammals, including representatives from the Black Hills.

Some reports of travel through the Black Hills in the mid-nineteenth century must be viewed with skepticism, because in those days the term "Black Hills" also applied to the Laramie Range along the North Platte River in Wyoming. For example, in 1856, Lieutenant F. T. Bryan and naturalist W. S. Wood were part of an expedition that was instructed to build a road from Fort Riley, Kansas, to Bridger's Pass, Wyoming (Bryan, 1858). Although they did not enter the Black Hills, some of the specimens of mammals collected by Wood bear this locality on the labels. Many books and articles have been published concerning the *Oregon Trail* of Francis Parkman in 1846; the numerous references to the Black Hills in these publications actually are applicable to the Laramie Mountains (Wade, 1947:393).

Hayden, with Captain W. F. Raynolds of the Yellowstone Expedition, passed through the northern Black Hills in 1859, reaching Devil's Tower on 20 July (Raynolds, 1868). Both the eastern and western margins of the Hills were reconnoitered by elements of the Powder River Expedition of 1865. In spite of the pressure to open up the Hills for exploitation of gold, the Indian Treaty of the Peace Council of Laramie, signed on 29 April 1868, gave that part of the Dakota Territory lying west of the Missouri River to the Sioux, temporarily closing the frontier.

Increasing rumors of gold in the Black Hills and continuing troubles with the Indians resulted in the expedition of Brevet Major General George A. Custer in 1874 (O'Hara, 1929; Jackson, 1966). Members of this expedition traveled about 600 miles in 60 days, and returned with numerous photographs, many observations on the natural history of the region, and gold from French Creek, Custer County. Dr. Othniel C. Marsh, the noted paleontologist, was invited to accompany Custer, but instead sent along his young assistant, George Bird Grinnell, who took notes on 34 species of mammals (Grinnell, 1875:79-84). The expedition entered the Hills from the north, traveling down Castle Creek, south to the Cheyenne River. It returned northward to the area around Harvey Peak, camping at French Creek near the present town of Custer, and then left the Black Hills by way of Boxelder Creek and Bear Butte. Ludlow (1875) gave an excellent report of the reconnaisance, and included two foldout maps of the routes of Warren in 1857, Raynolds in 1858, and Custer in 1874. The Newton-Jenney U. S. Geological Survey of 1875, with Colonel Richard I. Dodge commanding the military escort, spent five months in the Hills studying the geology and natural resources of the area (Jenney, 1878; Newton and Jenney, 1880). Due to ill health, C. G. New-

berry, the naturalist assigned to the expedition, was compelled to resign at Fort Laramie on the eve of departure; thus the only records of mammals (15 kinds) observed or taken on the trip were those recorded by Colonel Dodge (1876: 120-123, 128-134).

As the Black Hills opened to white settlement, biological exploration intensified. Wetmore (1968:215-216), and Pettingill and Whitney (1965:16-17) have reviewed botanical and ornithological investigations, respectively. In the summer of 1894, Walter W. Granger left the paleontological expedition sponsored by the American Museum of Natural History to the Badlands of South Dakota. He journeyed west to the Black Hills and collected 22 species of mammals, mostly from the southeastern and central sections (J. A. Allen, 1895a), including several undescribed kinds (J. A. Allen, 1894a, 1894b, 1895b). From 1899 to 1911, Henry Behrens made a collection of 30 kinds of mammals on his ranch along Spring Creek, and along the foothills south of Rapid City. Fifty-five of these specimens now are housed in the Pioneer Room of the Minnilusa Historical Museum in Rapid City, South Dakota.

The U. S. Biological Survey became active in the region at the turn of the century (Merriam, 1888, 1889, 1891). Vernon Bailey and Merritt Cary were responsible for obtaining mammals and natural history data from the region. Between 1899 and 1912, Cary (1917) periodically investigated the area along the South Dakota-Wyoming border in the vicinity of Elk Mountain. Bailey (1914) intermittently collected in the Black Hills from 1887 until 1913; observations of 25 species of mammals were made on his initial excursion near Rapid City and Deadwood late in 1887 (Bailey, 1888). The materials, gathered by Granger, Bailey and Cary contributed significantly to the present study.

A. H. Howell, N. Dearborn, and a field party from the U. S. National Museum worked in the central part of the Hills from mid-May to mid-June of 1910, and P. Moulthrop and G. W. Phillips from the Cleveland Museum of Natural History collected in the same area in August 1929 (Bole, 1935; Moulthrop, 1936). Victor H. Cahalane (1948, 1951), as Acting Chief of the Wildlife Division at Wind Cave National Park, compiled a partial list of mammals of that area in the course of field work from 15 August 1935 to 10 February 1936 (on file at Wind Cave National Park). Somewhat later, A. M. Stebler (1939) and L. R. Dice (1939) from the University of Michigan Museum of Zoology, initiated field investigations that resulted in published reports on mammals from the Black Hills. J. A. King (1951, 1955), also from the University of Michigan, worked in the central part of the Hills and at Wind Cave National Park at intervals from 1945 to 1952, and C. B. Koford (1958), from the Museum of Vertebrate Zoology, University of California, Berkeley, carried out investigations in the Wyoming sector, principally in the vicinity of Devils Tower.

In 1947, 1951, 1961, 1965, and again in 1967, field parties from the Museum of Natural History of The University of Kansas collected mammals in western South Dakota and northeastern Wyoming (Jones and Packard, 1958; Long, 1965; Jones and Genoways, 1967a, 1967b; Turner and Jones, 1968; Turner and Davis, 1970; White, 1952, 1953a, 1953b). My own work in the Black Hills began in the summer of 1965; I returned to the study area throughout the summers of 1967 and 1968. A week was spent in quest of hibernating bats in late November of 1967, and a week each in obtaining photographs and samples of soil in August of 1969, and March of 1970. In all, I was in the field for 31 weeks from mid-June 1965 to March 1970, including two months as a Ranger-Naturalist at Wind Cave National Park in 1968. Additionally, two weeks were required in 1968 to examine specimens from the Black Hills housed in museums other than at Kansas.

METHODS AND MATERIALS

Each of the six orders of Black Hills mammals and the 19 families (discussed briefly), including 44 genera and 62 species, are arranged in text following the arrangement of Hall and Kelson (1959). The species of each genus and, where appropriate, the subspecies of each species, are in alphabetic order. Keys to species, distribution maps, and enumeration of characters applicable to the various taxonomic categories, are not provided herein as these were deemed to be readily accessible in other publications.

The account of each monotypic species or subspecies native to the Black Hills incorporates the following:

1. The *scientific name*, employed in agreement with the International Rules of Zoological Nomenclature, and followed on the same line by the name of the author.

2. The *vernacular name*, in general accord with Hall (1965), and that which is considered appropriate for all subspecies of the given species.

3. The *synonymy*, in which the first citation is to the original description and is followed by designation of the type locality. The second citation is to the first usage of the currently accepted name-combination employed herein, unless that combination is identical to the name as originally proposed. In a few cases, a third citation is to a taxon described from the Black Hills, but now placed in synonymy.

4. The *distribution*, which concerns the regional distribution of each species and comments pertaining to the abundance and apportionment of each throughout the Black Hills. Included here are notations on ecological, altitudinal, and seasonal distributions; the latter is especially important for those mammals that hibernate or migrate.

5. Comments on *systematics* are included in most accounts. Comparisons of characters are made between the Black Hills populations and those of surrounding areas when these are warranted for taxonomic clarification or when conspicuous geographic variation is evident.

6. All *measurements*, external and cranial, are given in millimeters. Standard external measurements were read from labels attached to the specimens, excepting length of forearm; the latter is applicable only to bats and was measured from prepared museum specimens. Weights of adult males and non-pregnant adult females are given in grams. Stated measurements are the arithmetic mean, followed by the standard deviation. Unless otherwise stated, measurements are of adults only. Cranial measurements were taken to the nearest tenth of a millimeter with dial calipers in the manner described by Hall (1946:672-685), and Packard (1960:584-585); identical measurements were not taken for all species.

Variation in color was assessed by direct comparison of specimens and also by use of a Photovolt Photoelectric Reflection Meter, Model 610, utilizing red, green, and blue filters. Readings were taken from the middorsal region of museum study skins and could be repeated on the same individual with minimal variation. Samples of soil from various collecting sites were first dried for several hours in an oven, then subjected to color analysis with the reflection meter. Resultant measurements of reflected light were recorded for each skin and soil sample as percentage values of pure white calibrated against a standardized block of magnesium carbonate. These recorded measurements actually represent a composite value of both intensity of hue (that is, more red or less red in color) and tone (paler or darker in color). For example, pale brownish soils yielded higher reflectance readings when using a red filter than did dark reddish soils. Reflectance readings obtained from all three filters were summed in order to achieve an approximate index of tone. If, for instance, the specimens or soil samples were arranged in order of decreasing paleness of overall coloration, the resultant sequence derived by direct

comparison would be in agreement with the summed total (trichromatic) reflectance, or tone (Figs. 13 and 14). Intensity of each hue was derived by dividing the respective initial reflectance reading from each filter by the total reflectance readings from all three filters. Extremely greasy or damaged skins were not included in the color analysis.

In analysis of geographic variation, specimens were segregated by age, sex, season, and geographic origin. The measurements obtained under these groupings were then subjected to standard univariate statistical analysis and to an overall Analysis of Variance. If the Analysis of Variance indicated that significant differences existed among groups, then the Sums of Squares Simultaneous Test Procedure of Gabriel (1964) was applied in order to locate these differences.

7. Remarks on *autecology* ordinarily include information pertinent to the natural history of each species. Methods of capture, time of activity (i.e., Mountain Daylight Time, MDT, or Mountain Standard Time, MST), description of habitat, enumeration of associates, and additional noteworthy observations are recorded. A brief chronicle is given for those species that were common in historic times, but now have been reduced in numbers or extirpated. Reproductive data are summarized for each species for which information (usually taken from specimen labels or field notes of the collector) is available. Molt data were obtained from examination of museum specimens, both dry and in alcohol, by directing a stream of air through the pelage and noting the presence or absence of underlying new hairs. In recent year, specimens were examined in the field immediately after capture for ectoparasites. Parasites collected in this manner were preserved in 70 percent alcohol and referred to various specialists for identification. In compiling the above-mentioned data and observations, field notes of 46 individuals were consulted, in addition to my own firsthand observations.

8. The *records of occurrence*, include both *specimens examined* (based on 4727 specimens) and *additional records.*

Under *specimens examined*, the first notation is the total number of specimens examined by me, followed by the exact locality of capture, the number of specimens from each locality, and designation of site of specimen deposition. Localities are allocated to their respective counties, which are grouped under either South Dakota or Wyoming. County names and the localities within each county are arranged from north to south (and west to east if more than one locality occurs in the same latitude within a county). The many specimens examined for comparisons from areas surrounding the Black Hills are not enumerated. Abbreviations designating specimens examined in collections other than the Museum of Natural History of The University of Kansas are as follows: AMNH—American Museum of Natural History, New York; FMNH—Field Museum of Natural History, Chicago; MHM—The Pioneer Room, Minnilusa Historical Museum (collection of Henry Behrens), Rapid City; MSB—Museum of Southwestern Biology, University of New Mexico, Albuquerque; NRW—Collection of N. R. Whitney, Rapid City; SDMT—Department of Biology, South Dakota School of Mines and Technology, Rapid City; SDSU—Department of Entomology and Zoology, South Dakota State University, Brookings; UK—Department of Zoology, University of Kentucky, Lexington; UMMZ—Museum of Zoology, University of Michigan (including specimens formerly housed in the Cleveland Museum of Natural History), Ann Arbor; USD—Department of Biology, University of South Dakota, Vermillion; USNM—United States National Museum (including collections of the U. S. Biological Surveys), Washington, D. C.; UW—Department of Zoology, University of Wyoming, Laramie; WCNP—Collection of Wind Cave National Park, Hot Springs.

Additional records consist of reports

from the literature, specimens in collections that I have not examined, or identifications of presumed accuracy as recorded in card files of the U. S. Biological Survey (USBS); the abbreviation BB designates specimens in the collection of B. Bailey that were identified by personnel of the Survey. Localities from which specimens were examined are not duplicated in the additional records. Most sites from which mammals were obtained are shown in figure 2.

ENVIRONMENT

GEOGRAPHY

The Black Hills constitute a maturely dissected, isolated, mountainous region of approximately 4000 square miles that resulted from intermittent domal uplifts in Cretaceous, Miocene, and Pleistocene times. The area extends 120 miles in a northwest-southeast direction, and is 50 miles wide at the widest point. The Hills are entirely surrounded by the non-glaciated Missouri Plateau section of the Northern Great Plains physiographic province (Fenneman, 1931), and rise above the plains to an elevation of about 4000 feet on the east and 3000 feet on the west. The highest point (Harney Peak) lies 7242 feet above sea level. Most of the region lies within the drainage of the Cheyenne River, which circles the south end of the Black Hills, and the Belle Fourche River, which skirts the north edge of the area (Figs. 1 and 2).

As defined herein, the Black Hills are delimited by the distribution of Jurassic shale and sandstone of the Sundance Formation (Fig. 3). Thus, the region includes the Black Hills proper, as well as the Bear Lodge Mountains and Devils Tower of Wyoming; the latter two areas are closely allied with the Hills. Ranges of mountains nearest the Black Hills are the Laramie Mountains (elevations to 10,272 ft) and Big Horn Mountains (elevations to 13,165 ft); these lie approximately 150 miles to the southwest and west, respectively, in Wyoming.

GEOLOGY AND PHYSIOGRAPHY

As a result of the presence of a diversity of geological structures and productive mineral deposits, there are numerous publications concerning the geology of the Black Hills. The reader is directed to Darton (1909), Darton and Paige (1925), McIntosh (1931), Tullis (1951), and Gries and Tullis (1955) for detailed geological accounts of the region.

The Black Hills uplift is a crescent-shaped, anticlinal dome that rises several thousand feet above the surrounding Northern Great Plains (Figs. 1 and 3). The Central Basin is located slightly east of the main axis of the dome. It is a rugged mountainous core of Pre-Cambrian igneous rock and Pre-Cambrian, Paleozoic and Mesozoic sediments. The Basin is interspersed with park-like valleys and steep, narrow canyons that incline to the north, south, and east. In the Harney Peak-Needles-Mount Rushmore area (Fig. 4) there are bare granitic and metamorphic ridges. Encircling the Central Basin is the Limestone Plateau of rolling highlands (Figs. 5 and 10). The plateau is about two miles in width to the east, and reaches a maximum of 15 miles in width in the northwestern portion of the Black Hills. It is comprised of Paleozoic sediments (sandstone, shale and limestone) of the Deadwood, Whitewood, Pahasapa-Englewood and Minnelusa formations. The wall-like escarpment of the plateau reaches elevations of 7100 feet; it faces inward toward the Central Basin and is interrupted by such stream valleys as Sand, Cold Spring, and Spearfish creeks. In some areas (e.g., Big and Little Spearfish Canyons; Fig. 6) of the Limestone Plateau, high cliffs project above the valley floors. The rugged terrain in the northern Central Basin and northwestern Limestone Plateau was formed by solidification of igneous intrusions during Tertiary time (Fig. 3).

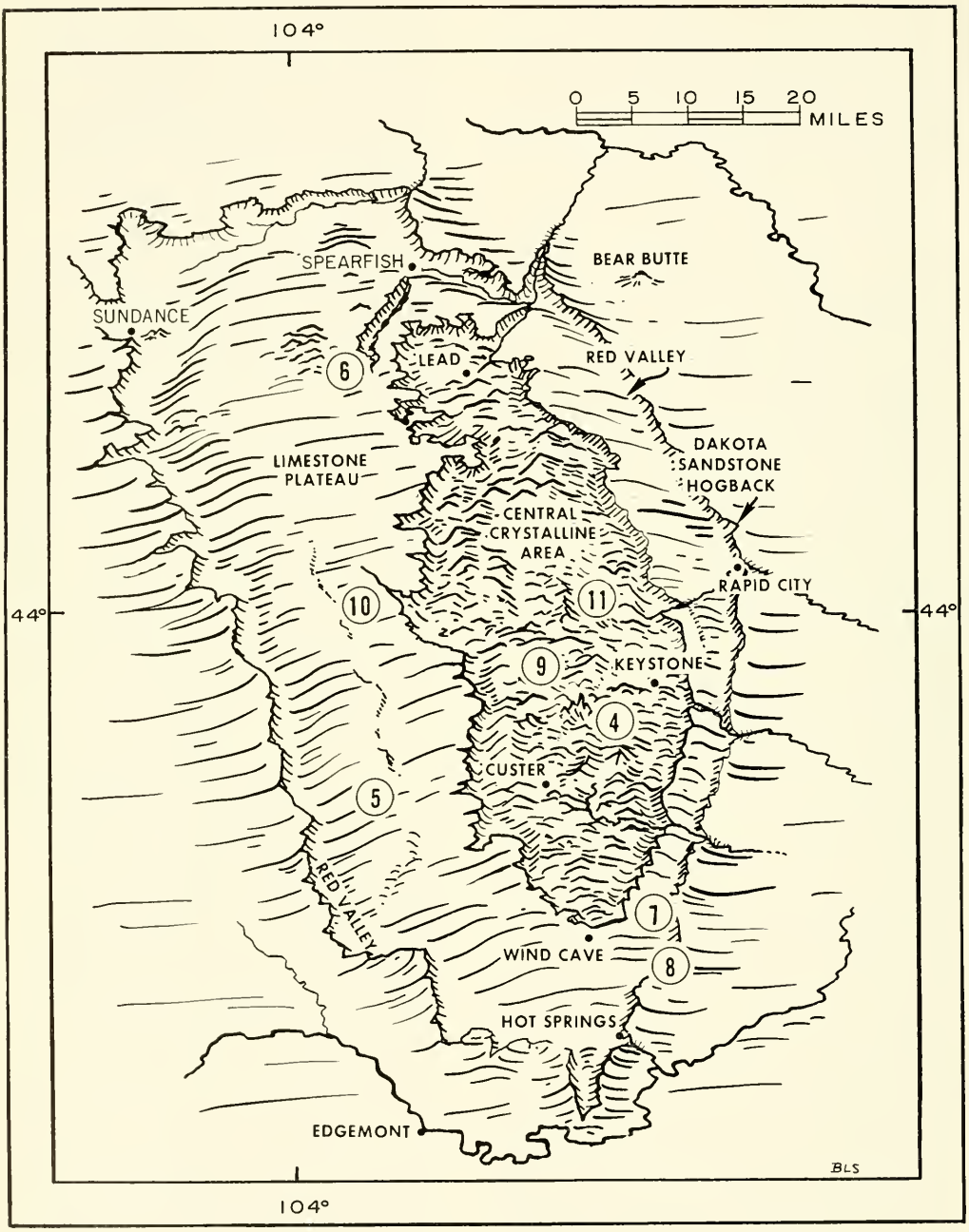


FIG. 1. General physiography of the Black Hills of South Dakota and Wyoming (modified after A. N. Strahler, *Physical Geography*, John Wiley and Sons). Encircled numbers indicate sites at which photographs of the corresponding figures were obtained.

Sloping outward from the plateau are broadly rolling tablelands that comprise the foothills and the Foothill Transition Soil Association (see SOILS section below). The foothills are less extensive along the eastern slope due to a steeper gradient, and are composed of Paleozoic limestone (Minnekahta Formation) and

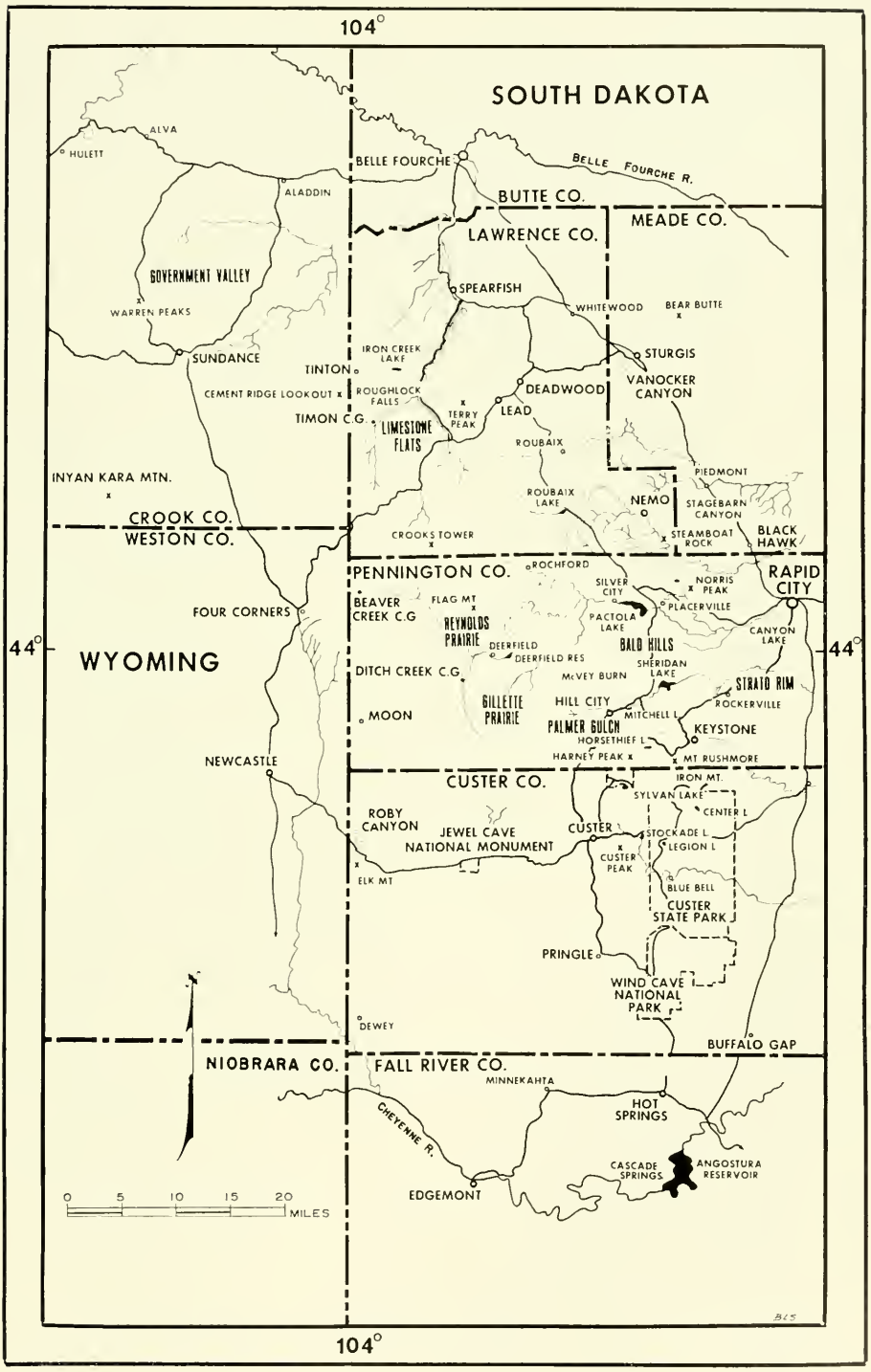


FIG. 2. General geography of the Black Hills, showing major collecting sites mentioned in text (modified after Pettingill and Whitney, 1965:frontis).

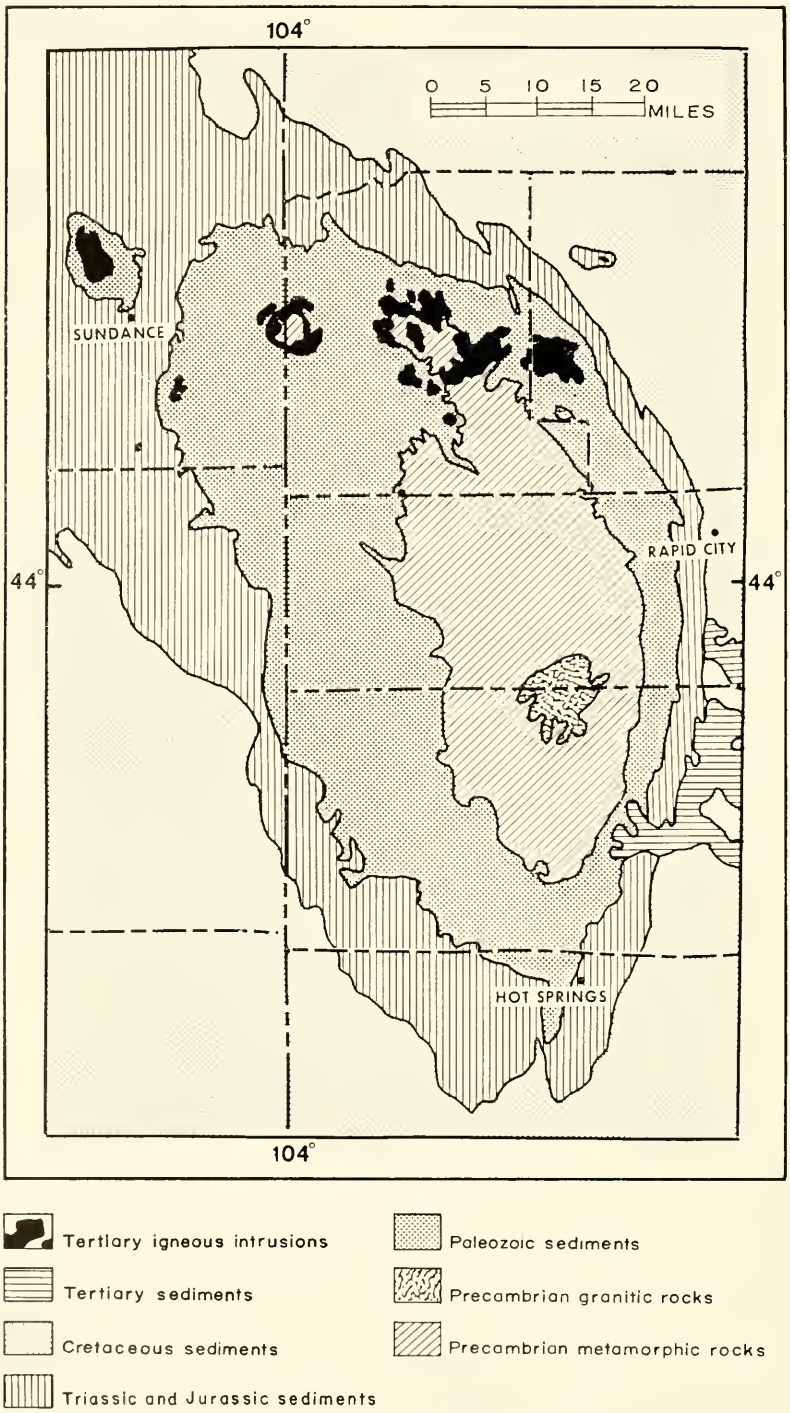


Fig. 3. Generalized geologic map of the Black Hills area (modified after Black Hills Area Resource Study, 1967:18).

shale (Opeche Formation). Along the base of the foothills lies a conspicuous, and remarkably continuous valley in the form of a "racetrack," which encircles the Hills (Fig. 7). This narrow trough represents the lowest elevation in the Hills (3200 to 3500 feet above sea level). It cuts into soft red shales and sandstone of the Spearfish Formation, which was formed as a deposition of sediments early in the Triassic. The Red Valley, so named because of reddish soils of the Spearfish-Neville Soils Subassociation, varies in width from a quarter of a mile (in the east) to more than six miles (in the northwest); the valley floor is dissected by many drainage divides that are separated by broad alluvial flats.

The Limestone Plateau, Central Basin, and peaks of the Bear Lodge Mountains form the so-called "boreal-cap" of the Black Hills; the latter two areas comprise the Mountainland Soil Association, whereas the former consists of the Limestone Plateau Soil Association. The boreal-cap is characterized by a predominantly coniferous forest fauna of boreomontane and cordilleran origin. Mammals such as Nuttall's cottontail (*Sylvilagus nuttallii*), the least chipmunk (*Eutamias minimus*), yellow-bellied marmot (*Marmota flaviventris*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), northern pocket gopher (*Thomomys talpoides*), red-backed vole (*Clethrionomys gapperi*), and long-tailed vole (*Microtus longicaudus*), reach their highest population densities in these areas. In the Central Basin, isolated grasslands of the Slate Prairie Soil Association (Fig. 11) are inhabited mainly by the white-tailed jackrabbit (*Lepus townsendii*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), deer mouse (*Peromyscus maniculatus*), and meadow vole (*Microtus pennsylvanicus*). The crystalline core near Harney Peak provides the restricted range of the introduced mountain goat (*Oreamnos americanus*). Both Nuttall's cottontail and the white-tailed jackrabbit are more abundant on the Limestone Plateau than elsewhere in the Hills. Because of the plateau's broad valley meadows and proximity to the foothills, it also provides optimal habitat for both the mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*). Streams transect all of these areas to produce the Undifferentiated Alluvial Soil Association that is inhabited by various riparian species such as the masked shrew (*Sorex cinereus*) and meadow jumping mouse (*Zapus hudsonius*).

Faunas of two isolated Tertiary igneous protrusions are noteworthy. Inyan Kara Mountain, surrounded by foothills and upland prairie in southeastern Crook County, Wyoming, is the primary range for a herd of recently introduced mountain sheep (*Ovis canadensis*) a species formerly native to the Hills (Baird, 1858: 678; Cowan, 1940:543). Devils Tower is an igneous monolith that protrudes 865 feet above the surrounding prairie and open pine woodland. The fissures and surface atop the Tower are well carpeted with lichens, grass, sagebrush, and prickly-pear cactus, and support a meager fauna consisting of least chipmunks, deer mice, and bushy-tailed woodrats (*Neotoma cinerea*) (exhibit, Visitor's Center, Devils Tower National Monument).

Higher areas in the foothills support a fauna that is similar to that of the boreal-cap, whereas the fauna of the lower regions more closely approaches that of the surrounding prairies. For example, along the foothill-Limestone Plateau border, the meadow vole often is captured in the same trapline with the long-tailed vole. Along the foothill-Red Valley transition, the meadow vole is associated with the prairie vole (*Microtus ochrogaster*), and the long-tailed vole is not present. Typical mammals of the Red Valley grasslands and lower foothills are the desert cottontail (*Sylvilagus audubonii*), white-tailed jackrabbit, thirteen-lined ground squirrel, black-tailed prairie dog (*Cynomys ludovicianus*), deer mouse, western harvest mouse (*Reithrodontomys megalotis*),

FIG. 4. The Needles, exposed crystalline rock in the Mount Rushmore-Harney Peak area of the Central Basin. These moss- and lichen-covered granitic ridges thrust upward nearly perpendicular to the surrounding forest, and comprise the restricted range of the introduced mountain goat.

FIG. 5. A broad upland valley on the rolling slopes of the Limestone Plateau, south of Moon. Such areas generally are farmed in oats, legumes and tame grasses, or are grazed, but also support large herds of deer.

FIG. 6. Due to resistence to erosion, high cliffs project as steep walls above canyon floors in more rugged areas of the Limestone Plateau, such as Little Spearfish Canyon. The above photograph was taken from the rear entrance of a cave, in a cliff above the Timon Campground, that served as a well-used night roost for several kinds of bats (see account of small-footed myotis).

FIG. 7. The Red Valley, locally termed the "racetrack," is a remarkably continuous trough that encircles the Black Hills, and occupies a valley-like position between the foothills and the Dakota Hogback. Large herds of bison, elk, and pronghorn, and colonies of prairie dogs inhabit the extensive grasslands comprising the Red Valley portion of Wind Cave National Park.

FIG. 8. The outer border of the Red Valley, and of the Black Hills, is formed by a steep-sided, 600-foot sandstone ridge, termed the Dakota Hogback, that slopes gradually outward onto the surrounding semiarid mixed grass prairie. The above break in the ridge (Buffalo Gap) has been eroded away by Beaver Creek as it flows out of the Black Hills. Large herds of bison and pronghorn previously migrated between the grasslands of the Red Valley and those of the Northern Great Plains through this stream gap, which also provided access for Jedediah Smith in 1823 and later explorers and adventurers.

FIG. 9. The predominant vegetational component of the Black Hills, especially in the Central Basin, is a montane belt of ponderosa pine. This conifer seems tolerant of xerophytic conditions and grows even on exposed rocky ridges. The dark appearance of the foliage of the ponderosa pine, when viewed from a distance, accounts for the Sioux Indian name *Paha Sapa,* or "Black Hills."

FIG. 10. Moist, narrow valleys in the Limestone Plateau support a dense subalpine belt of white spruce with an associated understory of northern affinities. Luxuriant riparian habitats such as that bordering the Beaver Creek Campground are occupied by masked shrews, meadow jumping mice, and several kinds of voles.

FIG. 11. The Bald Hills is one of three isolated grasslands in the Central Basin situated on well-rounded slopes underlain by slates. There is no evidence that these grasslands have ever been forested (Photograph by Barry L. Siler).

prairie vole, badger (*Taxidea taxus*), and coyote (*Canis latrans*). In addition to those species just mentioned, the Sandhill Regosol Soil Subassociation along the Custer County, South Dakota-Weston County, Wyoming border is inhabited by several heteromyids. Included among the latter are the hispid pocket mouse (*Perognathus hispidus*), olive-backed pocket mouse (*P. fasciatus*), and Ord's kangaroo rat (*Dipodomys ordii*); all are characteristic of rocky or sandy soils.

The outer border of the Red Valley is formed by a 600 foot sandstone rim that is steep-faced within, but slopes gradually outward onto the surrounding Great Plains (Fig. 8). This hogback ranges in elevation from 3800 to 4900 feet (near Elk Mountain). The outward-sloping cuestas frequently are broken by streams. The inner face of the hogback is of Jurassic age and is composed of green shales and red sandstones of the Sundance Formation and to a lesser extent of the shales, sandstones, and limestones of the Morrison Formation. The outer slope is judged as Cretaceous in age and formed of the Skull Creek and Inyan Kara formations, both of which are composites of Dakota and Lakota sandstones, Fuson shale, and Minnewaste limestone formations. The conspicuous hogback, marking the boundary between the Black Hills and the Northern Great Plains, forms a series of ridges that were an obstacle to early travelers. Beaver Creek has eroded away a break in the hogback, just northwest of Buffalo Gap. It was through this stream gap that large herds of bison (*Bison bison*) previously migrated into the grasslands of the Red Valley.

CLIMATE

The climate of the Black Hills is distinct from that of the surrounding, semi-arid Great Plains in being more moist and less subject to extremes of temperature. Because of warm "chinook" winds and frequent sunny skies, the Black Hills are the warmest part of South Dakota in winter. An additional moderating influence is the tendency for heavy colder air to seek low elevations; thus, Arctic air masses that blanket the plains in colder winter months bypass the higher elevations of the Hills. Conversely, summer temperatures at higher elevations in the Hills are cooler than are those of the surrounding prairies.

Contrasts in climate between Lead, in the north-central part of the Black Hills, and Hot Springs, at the southern periphery, are shown in table 1 and figure 12. Average maximum temperatures for July range from 81-83°F in the Black Hills and 88-92°F on the adjacent plains; average minimum temperatures for January range from 9-14°F in the Hills and 4-9°F on the surrounding grasslands. Warm days and cool nights are characteristic of the Hills. Air temperatures usually have a daily range from 50-60°F in the shade in summer, but the range may reach 80°, or more, in direct sunlight (Wetmore, 1968:217).

TABLE 1.—Temperature and precipitation data for Hot Springs (southeastern Black Hills) and Lead (north-central Black Hills), 1931-1935 (Hodge, 1960:8).

Climatological station (with altitude)	Temperature (°F)					Precipitation (inches)			
	Highest recorded temperature	Highest monthly mean	Lowest recorded temperature	Lowest monthly mean	Annual mean	Highest monthly mean	Lowest monthly mean	Mean annual precipitation	Mean annual snowfall
Hot Springs (3535 feet)	112	75.3 (July)	—41	25.1 (January)	48.8	3.04 (May)	0.36 (December)	16.06	36.4
Lead (5245 feet)	101	69.7 (July)	—40	24.3 (January)	44.9	4.09 (June)	0.87 (February)	23.81	100.1

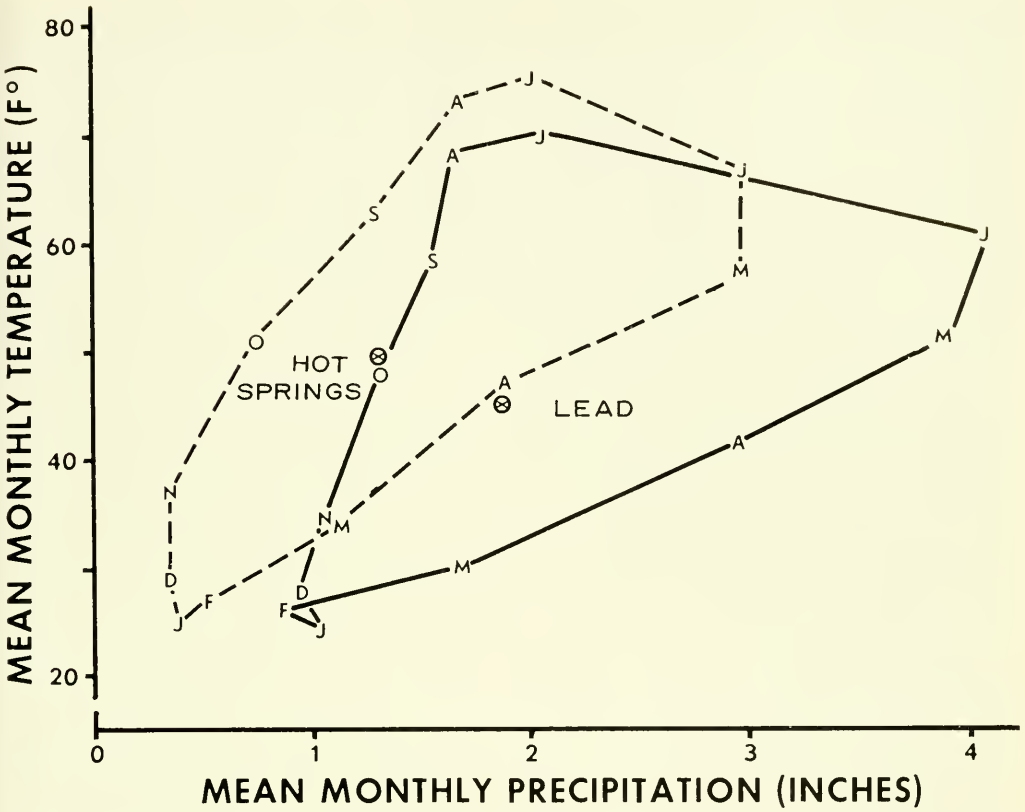


FIG. 12. Hydrothermograph for Lead (solid line) in the north-central Black Hills, and Hot Springs (broken line) in the southeastern Black Hills, 1931-1935 (Hodge, 1960:8). Labeled circles (×) indicate annual means of both parameters for each climatological station.

The frost-free season is shortest at higher elevations, where brief freezing has been known to occur at any time of summer; however, there are usually only 110 frost-free days in the Black Hills as compared to 130 on the pheripheral prairies.

Average annual precipitation in the Black Hills ranges from 16 inches, in the southern portion, to 28 inches in the northern section, where snow and rain often are formed when prevailing winds are forced abruptly up steep sides of mountains. Mean annual precipitation on the adjacent plains is 14-16 inches. Much of the total precipitation occurs as rain during summer in the drier southern portion of the Hills, whereas it is much more evenly distributed throughout the year in the moister northern section. Hailstorms generally occur in midsummer, and lightning usually in late summer.

SOILS

Materials from which soils have developed in the Black Hills include ancient crystalline rock in the central part of the region and sedimentary rocks (shale, sandstone, and limestone) in outlying areas (Figs. 1 and 3). Local topography contributes to soil formation by determining drainage; thus, steep slopes have well-drained, thin soils, whereas more level areas have more poorly drained, deep soils.

The major soils of the Black Hills are the Gray Wooded Soils; they are unique to the general region because they de-

veloped under forest in a relatively humid climate. Soils of the surrounding area developed under grasslands in a climate ranging from moist subhumid to semiarid. The horizons of Gray Wooded Soils of the Black Hills are subdivided as follows: 1) A_{00} (forest litter), A_{01} (partly decayed litter), and A_{02} (well decayed litter); these are horizons which are organic and thin (i.e., one-half to two inches in depth). 2) A_1—a mineral horizon that is thin or absent. 3) A_2—a horizon that is weakly platy in structure and from four to 12 inches in depth. 4) B_1—a four-inch-thick transitional layer between the A_2 and B_2 horizons; B_1 is absent in the Hills. 5) B_2—a horizon which is brown and blocky in structure and possesses clayfilms on all surfaces; this layer is between 10 and 30 inches in depth. 6) C—a horizon which varies in composition in different areas.

Other zonal soils that occur on lower slopes are the Chernozems and Chestnut soils. Color of the surface layer of the Chernozems is black to dark, grayish brown. Soils of this type occupy open woodlands and are paler in color and browner in the southern part of the Hills than in the northern sections. A_1 horizons usually are five to eight inches in depth and granular in structure. B_2 horizons are about eight to 10 inches in depth and structured of prisms that ordinarily are coated with clayfilms on all surfaces. B_3 horizons have a weak, prismatic structure; they are usually more than six inches in depth and more clayey in composition. Both the B_3 and C horizons are enriched with lime leached from the upper layers. The surface layer of Chestnut soil is brown or reddish in color and developed under grasslands. The A_1 horizon is organic and about two to four inches in depth. The B_2 horizon is between 10 and 15 inches in depth and of prismatic structure with clayfilms on most surfaces. The B_3 horizon is at least six inches in depth and structured of prisms. Both the B_3 and C horizons contain free carbonates.

Azonal soil groups in the Black Hills include Regosols, Lithosols, and Alluvium. Regosols are thin soils developed in unconsolidated material, whereas Lithosols are thin soils over solid rock (within 18 inches of the surface). These immature soils occupy steep slopes where runoff is so excessive that little leaching or development of humus occurs. No true subsoil is present. Alluvium occupies flood plains of various water courses in the Hills. Alluvium tends to be darker and more humic than soil of the adjacent uplands and frequently supports a notably different riparian plant community.

A great need exists for detailed information on soils in the Black Hills. Most of the soils are unclassified and are stony or rocky, reflecting the local geology and physiography. For detailed information concerning land use of the soil associations, the reader is directed to Austin (1965:26-28), Westin *et al.* (1967:1-32) and to miscellaneous publications issued by the Soil and Water Conservation Districts of the respective counties. Some relationships of soils to the distribution and speciation of mammals in the Black Hills are discussed beyond.

The following description of Soil Associations in the Black Hills (referred to in text) has been synthesized from fragmentary literature and in consultation with the South Dakota Soils and Water Conservation Service.

Mountainland Association.—occupies the Central Basin mountainous core (1200 square miles) of igneous and sedimentary rock; excessively drained; topography: high rocky ridges, narrow rolling plateaus, deeply entrenched canyons, and park-like mountain valleys; exposed slopes: bare rock; steep slopes: Spearfish and Laporte Lithosols; upper forested slopes: Edloe Gray Wooded Soils; intermediate woodland slopes: Chernozem Soils; lower grassland slopes: Chestnut Soils; along valley and canyon drainages: -Table Mountain Soils (alluvial loams, intermixed with loose stones); land use: recreation, major timber production (ponderosa pine), and grazing.

Limestone Plateau Association.—occupies a high plateau of sedimentary rock (sandstone, limestone and shale) that encircles the Central Basin; well-drained; topography: rolling slopes,

broad upland valleys, few rocky ridges, buttes and steep canyons; distribution of major soil types as in the Mountainland Association, differing only in percent coverage due to contrasts in topography; rocky silt loams that occupy ridges may be absent on south-facing slopes where stands of pine are thin or absent; grassland soils of some upland valleys have a water table; land use: recreation, some timber production (ponderosa pine and white spruce), grazing, and farming (oats, legumes and tame grasses).

Slate Prairie Association.—occupies three isolated prairies (Reynolds and Gillette Prairies, and the Bald Hills) comprising about 9000 acres in the Central Basin; well-drained; topography: rolling to steeply rounded slopes; shallow rocky loams underlain by slates, some Table Mountain Soils along upland drainages; no evidence of prior forestation; land use: grazing and farming (oats and vegetables).

Undifferentiated Alluvial Association.—occurs along stream channels of all major valley systems in the Black Hills; well-drained, except for some areas of seepage; topography: fairly level to gently undulating; deep silt loams, with weak subsoil development; land use (highly productive, but limited by cool temperatures and short growing season): grazing and farming (oats, alfalfa and hay).

Foothill Transition Association.—intervenes between the Limestone Plateau and Dakota Hogback; well-drained; topography: complexly dissected foothills with gently rounded to steep slopes, and narrow ridges and valleys; land use: recreation, minor timber production (ponderosa pine), grazing, and dryland and irrigational farming. Due to topographical diversity, this region is divided into several subassociations:

Laporte-Sandoz-Berthoud Subassociation.—calcareous soils with limestone outcrops often exposed on the surface; Laporte Lithosols: occur on ridge tops and abrupt slopes; Sandoz Chernozems: occupy intermediate woodland slopes; Berthoud Chestnut Soils: occupy alluvial swales and drainageways on lower grassland slopes.

Spearfish-Neville Subassociation.—reddish-colored Chestnut Soils under grasslands that occupy a valley-like ("race-track") position between the steeper foothills and Dakota Hogback and overlay a gypsum-like shale substratum; Spearfish Soils: occur on gently rolling slopes; Neville Soils: occupy longer and smoother colluvial and residual slopes.

Sand Hill Regosol Subassociation.—sands and fine sandy loams (presumably of the Valentine series) extend northwestward from the Sand Hills of Nebraska, along the Custer County, South Dakota-Weston County, Wyoming border; occur on gently rolling terrain; exposed rock prominent in some areas.

Dakota Hogback Association.—occupies a steep sandstone ridge that encircles the outer limits of the Black Hills; well-drained; topography: abrupt to sloping, with exposed sandstone outcrops; shallow calcareous Travessila Lithosols; land use: grazing.

The *Pierre Shale Plains Association* occurs just exterior to the Black Hills, consisting of grassland Chestnut Soils with moderately deep firm clays overlaying shales, and is penetrated by the *Vale-Beaverton Alluvial Association* that occupies low terraces and benches adjacent to larger streams that flow out from the Hills. Soils of Southwestern South Dakota, excluding the Black Hills, have the palest tone, are browner in hue, and have less organic matter and total nitrogen than soils of other parts of the state.

HYDROGRAPHY

Description, classification, and utilization of lakes and streams in the Black Hills have been discussed in the Black Hills Area Resource Study of 1967, and by Stewart and Thilenius (1964). All water courses that arise in the Black Hills comprise 1302 miles of stream drainage, and empty either into the Belle Fourche or Cheyenne rivers; both rivers originate on the gently rolling plains to the west in Wyoming. The Belle Fourche River, with a surface drainage of 7210 square miles, borders the northern margin of the Hills; whereas, the Cheyenne River, with a surface drainage of 2000 square miles, flows along the southern periphery. Together, these rivers have an annual flow of 522,000 acre-feet; they join on the prairie about 60 miles east of the Black Hills and flow eastward (as the Cheyenne) into the Missouri River. The northwest-southeast alignment of their major tributaries, such as Boxelder, Rapid, Spring, Battle, French, and Beaver creeks and of other streams in western South Dakota, coincides with the prevailing wind direction, and appears to be the result of periodic accumulation of locally derived eolian sediments

(White, 1961:207). Although June is the time of maximum precipitation, maximum surface runoff is in May owing to the greater evapotranspiration rates encountered later in the growing season. Floods are common in both months.

Due to abrupt topographic relief, most streams in the Black Hills are radial-dendritic systems that flow swiftly; only in a few montane meadows and broad valleys does a more gradual gradient allow some meandering and formation of small, semimarsh areas adjacent to stream channels. In addition to aquatic mammals such as the beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*), riparian species such as the mink (*Mustela vison*), masked shrew, jumping mouse, long-tailed vole, and meadow vole inhabit these moist environs.

When European man first entered the Black Hills, beaver ponds were the only sources of standing water. Now the foothills are interrupted by thousands of small reservoirs that store water for livestock and for fish and wildlife; major impoundments such as Angostura, Deerfield, Pactola, Keyhole, and Belle Fourche reservoirs also have been constructed. These artificial bodies of standing water (usually located over shist or shale) are used for recreation, as well as for watershed development and irrigation.

Except for the headwaters, all streams in the Black Hills are affected to some degree by pollution. Whitewood Creek is the most severely polluted stream in the Hills; it carries an extremely high content of rock-flour and chemical pollutants from mining operations and a heavy load of municipal wastes from Lead and Deadwood. The North Fork of Rapid Creek also is polluted with a high content of bog-iron wastes. Stockade Lake is of poor quality due to sewage effluents from Custer. A dense bloom of a toxic blue-green algae (*Aphanizomenon flos-aquae*) results from the supplemental nitrogen and phosphorous, and drastically reduces productivity of the lake (Stewart and Thilenius, 1964:46).

Dodge (1876) recorded the hydrography of the Black Hills when he accompanied the Newton-Janney U. S. Geological Survey of 1875. Stream flow was reported as substantial and the waters as being "cool, clear, and pure." Although riparian vegetation was sufficiently dense to impede travel along the stream bottoms, forest cover evidently was less extensive then than now, in that large older trees were "scarcely to be found." Adequate fire protection and management practices such as "thinning" have allowed a mature forest with a closed canopy to develop over much of the Hills. Thickening of the forest, with resultant interception of precipitation and increased evapotranspiration, is the greatest single factor in reduction of total surface discharge and in decrease of moisture available for recharging ground water stores (Stewart and Thilenius, 1964). Trampling of riparian vegetation by cattle around springs and creeks, construction of roads along stream channels, tapping of ground water supplies with wells, storage and utilization of water for agriculture and industry, and deposition of tailing from mines, tannic acid from saw mills, and wastes from municipalities continue to degrade aquatic habitats in the Black Hills.

VEGETATION

The most conspicuous component of the Black Hills vegetation is the coniferous forest, which is dominated by a montane belt of ponderosa pine (*Pinus ponderosa*) (Fig. 9). In more mesic sites on northern exposures in the Central Basin and on the Limestone Plateau, there is a subalpine belt of white spruce (*Picea glauca*) with an associated understory of plants with northern affinities (Fig. 10). Kentucky bluegrass (*Poa pratensis*), introduced from Europe in the 17th Century, is the predominant graminoid plant of the open meadows, parklike areas, and grasslands of the foothills and Red Valley. The flora is a mixture of boreal,

cordilleran, eastern deciduous forest, and Great Plains species (Rydberg, 1896; Webb, 1965). Biogeographic affinities of the Black Hills biota have been treated by various authors. Birds are discussed by Miller (1941), Pettingill and Whitney (1965), and Mengel (1970). Byers (1961) and Ross (1965; 1970) dealt with insects, and Smith (1957) discussed the smooth green snake. Willows and lichens were treated by Froiland (1962) and Wetmore (1968), respectively. Forest and other vegetational components are discussed by Buttrick (1914), Halliday and Brown (1943), Hayward (1928), McIntosh (1931), Dillon (1956), Potter and Green (1964), and Watts and Wright (1966).

The most exposed sections in the Black Hills, such as the crown of Harney Peak and the Needles section, either are devoid of vegetation or support bryoids (mosses) and thallophytes (lichens). A climatic timberline is not present; instead, the absence of trees along the high summits is due to lack of soil and to extreme exposure. In general, three vegetational types occur in the Black Hills—coniferous forest, deciduous woodlands, and prairie grasslands. Dry slopes are dominated by ponderosa pine, the dark appearance of which accounts for the Sioux name *Paha Sapa* or "Black Hills." Usually broadleafed trees are developed mainly along drainage channels, or are present as groves on old, burned areas. Grasslands are found mostly on slopes of the foothills, but also in isolated prairie areas even at higher elevations.

Coniferous Forest Association.—This association forms a forest that is dominated by ponderosa pine, which appears to be extremely tolerant of xerophytic conditions (Fig. 9). The species ranges between elevations of approximately 3500 and 7000 feet, and forms parklike forests at higher elevations that give way to open woodlands at lower elevations. On the pine-clad uplands, the soil is coarse, well drained, and quite warm in the summer. In the western section, and especially on the hogback, western red cedar (*Juniperus virginiana*) intrudes among the pine. Along the cooler canyon floors and northern slopes of the central and moist northern sections of the Black Hills, the coniferous forest includes white spruce, paper birch (*Betula papyifera*), and quaking aspen (*Populus tremuloides*). The accompanying understory consists of wild sarsaparilla (*Aralia nudicaulis*), twin-flower (*Linnaea borealis*), swamp currant (*Ribes lacustre*), bunchberry (*Cornus canadensis*), red osier (*C. stolonifera*), Venus' slipper (*Calypso bulbosa*), squashberry (*Viburnum edule*) buffaloberry (*Shepherdia argentea*), and huckleberry (*Vaccinium membranaceum*) in close association. White spruce may occasionally dominate the coniferous forest of lower slopes in these areas, but usually it occurs in subalpine belts that are in close proximity to montane belts of ponderosa pine (Fig. 10). Predominant associates of the pine are various bunch grasses, bearberry (*Arctostaphylos uva-ursi*), wild rose (*Rosa acicularis*), creeping juniper (*Juniperus horizontalis*), ground juniper (*J. communis*), Oregon grape (*Berberis repens*), redroot (*Ceanothus velutinus*), New Jersey tea (*C. ovatus*), and poison ivy (*Rhus radicans*).

Deciduous Woodland Association.—Bur oak (*Quercus macrocarpa*) commonly is intermixed with the pines along drainages near the periphery of the Hills; it occurs in drier valleys, on drier slopes, and on sandy to gravelly soils. Quaking aspen, paper birch, green ash (*Fraxinus pennsylvanica*), and American elm (*Ulmus americana*) are also present. In the northern section, and especially in the Bear Lodge Mountains, bur oak is the dominant tree growth on many slopes leading away from stream channels. The oak has an undergrowth of hawthorn (*Crataegus chrysocarpa*), chokecherry (*Pyrus virginiana*), hop hornbeam (*Ostrya virginiana*), and poison ivy.

Riparian Association.—Streamside habitats in the Black Hills are characterized by fluviatile soils that are cool, moist, and somewhat more finely tex-

tured than that of the pine-clad uplands. These habitats support American elm, cottonwoods (*Populus deltoides*), box-elder (*Acer negundo*), willows (*Salix* sp.), serviceberry (*Amelanchier alnifolia*), red-berried elder (*Sambucus pubens*), blue flag (*Iris missouriensis*), Solomon's seal (*Polygonatum biflorum*), carices (*Carex* sp.), and rushes (*Juncus* sp.).

Mountain Prairie Association.—On a few rolling uplands at fairly high elevations, an isolated prairie type of habitat develops in areas where soil texture, moisture, and depth reach a favorable balance. Examples of these grasslands are the Gillette and Reynolds prairies, and the Bald Hills (Fig. 11). Green needlegrass (*Stipa viridula*), western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloura gracilis*), timothy (*Phleum pratense*), red-top grass (*Agrostis palustris*) and brome grass (*Bromus* sp.) occur with silver sagebrush (*Artemisia cana*), brittle pricklypear cactus (*Opuntia fragilis*), common pricklypear cactus (*O. compressa*), plains pricklypear cactus (*O. polycantha*), pincushion cactus (*Coryphantha missouriensis*), goldenrods (*Solidago* sp.), Indian paintbrush (*Castilleja sulphurea*), mariposa lily (*Calchortus nuttallii*), gland stem (*Adenocaulon bicolor*), and asters (*Aster* sp.).

Great Plains Prairie Association.—Many tongues of the surrounding plains extend into the Hills, especially from the south. The prairie-forest border is between 3500 and 4000 feet in elevation. Graves (1899) indicated that in areas where trees occur in valleys and on north-facing slopes, the prairie-forest border is natural. However, at localities where trees occur on ridges instead of valleys, the prairie-forest border probably is due to fire. Prairie grasslands formerly prevailed in the Red Valley. Vegetation of the prairie is far from uniform in its composition. Dominants among the grasses are western wheatgrass, green needlegrass, blue grama, sideoats grama (*Bouteloura curtipendula*), little bluestem (*Andropogon scoparius*), big bluestem (*A. gerardi*), needle and thread grass (*Stipa comata*), porcupine grass (*S. spartea*), buffalo grass (*Buchloe dactyloides*), Indian grass (*Sorgastrum avenaceum*), and Kentucky bluegrass. Forbs include pricklypear cactus, pin-cushion cactus, soapweed (*Yucca glauca*), sweet clover (*Melilotus officinalis*), blue vervain (*Verbena hastata*), lamb's-quarters (*Chenopodium album*), sunflowers (*Helianthus* sp.), harebell (*Campanula rotundifolia*), western salsify (*Trogonpogon dubius*), prairie sandreed (*Calamovilfa longifolia*), skunkweed (*Croton texensis*), scarlet gaura (*Gaura coccinea*), and wild alfalfa (*Psoralea tenuiflora*). Dominant browse species are chokecherry, skunkbush sumac (*Rhus trilobata*), wormwood sagebrush (*Artemisia dracunculus* and *A. dracunuloides*), fringe sagebrush (*A. frigida*), mountain mahogany (*Cercocarpus montanus*), western sandcherry (*Prunus besseyi*), and wild rose (*Rosa woodsii*). Scientific names of plants in the resumé follow the usage of Wetmore (1968) and Pettingill and Whitney (1965), whereas vernacular names generally follow the usage of Over (1932). Professor Ronald L. McGregor and associates at The University of Kansas currently are studying the flora of the Black Hills region, and I am grateful to them for verifying the nomenclature or suggesting appropriate changes for use here.

PLEISTOCENE HISTORY

Pre-Wisconsin Events.—The Pleistocene Epoch was characterized by a series of climatic fluctuations throughout the world. (At least four southern cool pluvial periods occurred concurrently with northerly continental glaciation. Subsequent to each of these episodes, a comparatively warm, dry interglacial interval followed.) As a consequence of these oscillations, distribution and speciation of many elements of the boreal and temperate biotas were markedly affected.

Prior to the Pleistocene, mountain-

building in the Rocky Mountain region probably created a rain shadow in the Black Hills region. Further uplift during the Pleistocene caused entrenchment of streams around the edge of the Hills (Darton, 1909). Previously, the Cheyenne River and other streams to the south of the Hills probably flowed toward the Gulf of Mexico. Thus, the present course of the Missouri River had not yet been attained (Flint, 1955; Lemke *et al.*, 1965).

Because of relatively low elevation and low precipitation, montane glaciers did not form on the Black Hills (Hayward, 1928; McIntosh, 1931). Nonetheless, Darton (1906) and others reported that Cordilleran glaciers formed in the Bighorn Mountains between 9500 and 11,000 feet and flowed down to 6500 feet. There is no evidence that continental glaciers entered Wyoming (Long, 1965), but at its maximum, about 18,000 BP, the Wisconsin ice sheet terminated about 150 miles east of the Black Hills (see below), and that part of South Dakota west of the Missouri River escaped direct glacial action (Flint, 1957). Intense frost evidently occurred within 50 to 100 miles of the ice sheet, making the Hills region subject to periglacial influences. Erosion, deepening of stream channels, deposition of sands and gravels, and development of soils also occurred in that region during the late Pleistocene.

The Nebraskan and Kansan glaciations covered most of South Dakota east of the Coteau du Missouri, whereas the Illinoian glacier reached only the extreme southeastern corner of the state, near Hartford (Lemke *et al.*, 1965). This record is based principally on till found overlying presumed Pearlette Volcanic Ash of late Kansas or Yarmouthian age (Schultz and Smith, 1965). Distribution of Pre-Wisconsin till indicates that glaciers advanced chiefly via the James River and Red River lowlands. The Wisconsin ice front, as evidenced by accumulation of drift deposits, extended from southeastern South Dakota, northwestward toward North Dakota, just west of the Missouri River, roughly paralleling the river channel (Flint, 1957).

Apparently, these glacial periods were characterized by cool, moist conditions that resulted in the southward displacement of a northern biota. Fossil remains of typical Hudsonian and Canadian zone mammals (including various shrews, microtines, sciurids, caribou, muskoxen, moose, and the marten) have been described from Wisconsin deposits far to the south of their present distributions (Banfield, 1962; Barbour, 1931; Benninghoff and Hibbard, 1961; Cushing, 1945; Findley, 1953; Guilday, 1967; Hay, 1923, 1924; Hibbard, 1949, 1970; Hibbard and Hinds, 1960; Jakway, 1958; Murray, 1957; Schultz, 1934; Schultz *et al.*, 1951; Semken *et al.*, 1964; Skinner, 1942; Stearns, 1942; Wilson, 1967). There is good evidence that during a part of each interglacial period (Aftonian, Yarmouth, and Sangamon), subtropical climates extended farther northward than now (Hibbard, 1960). Subsequent transition to subhumid, mesothermal climate led to each following glacial episode.

Bergmann's Rule states that within a given species of warm-blooded animal, body size increases with latitude, thus implying an adaptation that presumably serves to decrease the surface to volume ratio, thus conserving body heat in cold environments. Guilday *et al.* (1964), Hibbard (1963), and Parmalee (1967) presented evidence of shifts in populations in some late Pleistocene faunas in response to climatic change; thus, larger northern taxa were replaced by smaller southern relatives coincident with amelioration of cool post-glacial climatic conditions. Modern representatives of these same species display a similar pattern of variation.

Although details are conjectural, evidence of the displacement of biotic assemblages during the Pleistocene seems impeccable. Voss (1939) estimated that the biota inhabiting four million square miles was either obliterated or displaced during this period. Amelioration of climate during the interglacial stages al-

lowed migration northward; reversal of climatic trends during glaciation resulted in displacement southward. Some isolated relict colonies were left in favorable or tolerable locations along the various routes of dislocation (MacGinitie, 1959).

Massive shifts of biotic assemblages occurred several times in response to changing climates and resultant glaciation. Although the sequence of events for each glacial episode and subsequent interglacial stage presumably was similar, it is necessary to consider only the effects of the last continental glacier and ensuing post-glacial events (including additional minor oscillations) to explain the composition of the Recent biota on the Black Hills. Effects of temporary isolation imposed by Pre-Wisconsin glaciations would have been damped by reinvading elements through genetic swamping that would be permitted by the next advance and retreat. Much of the biota on the Hills is endemic at the subspecies and varietal levels of divergence. Had the current biota been effectively and totally isolated by Pre-Wisconsin episodes, endemism at the species level presumably would be more predominant in the Black Hills. In addition, the warm hiatus of each interglacial stage seemingly would have affected the boreal and montane components adversely, causing extensive extirpation and eliminating potential centers of dispersal.

Wisconsin Events.—The precise climatic conditions in South Dakota and Wyoming during maximal continental and Cordilleran glaciations remain open to question. Dillon (1956:168) proposed that dry, cold expanding air masses descended off the icecap as a result of anticyclonic circulation. This resulted in a mean annual rainfall of about 10 inches in the periglacial regions. However, the pollen spectrum provides evidence of a somewhat more mesic environment on the Northern Great Plains during maximal glaciation. The northern ice sheet was an impediment to the southward flow of cold Arctic air onto the plains (Bryson *et al.*, 1970); thus, winters were warmer than at present. Absence (or only weak development) of hot dry westerlies, which did not begin to increase in strength and effect until the beginning of the Boreal Period (Bryson and Wendland, 1967), resulted in cooler, more moist summers than at present. In postulating climates and life-zones coincident with Wisconsin glaciation, Dillon (*loc. cit.*) proposed a depression (from the present) of 10-25° F in mean annual temperature for the unglaciated portion of the Northern Great Plains. His proposal is based on the assumption that 45° was the mean maximum temperature under which a glacier could continue growth. Because of their higher elevation, the Black Hills currently are cooler in summer, warmer in winter, and receive greater annual rainfall than do the surrounding plains. Therefore, climatic conditions suggested for the plains during Wisconsin time may be somewhat extreme for the Hills, which presumably would have been more mesic and less subject to wide seasonal fluctuations in temperature than other periglacial regions.

Speculation has varied concerning the nature of the vegetation immediately bordering the ice sheet. Tundra (Martin, 1959; Watts, 1967), grassland (Shimek, 1948; Kendeigh, 1961; Frey, 1965) and forest (Clements and Chaney, 1937; Flint, 1957; Byers, 1961) have been assigned to the periphery of the ice front.

Rudd (1951) postulated that the continental plains were too cold and dry to support continuous forest during glaciation. The forested margins of present-day montane glaciers and the previously mentioned evidence for warmer winters and more mesic summers on the plains during maximal glaciation contraindicate Rudd's proposal.

Potzger and Tharp (1947) and Deevy (1949) first emphasized the biogeographical implications of spruce pollen occurring far south of its present distribution during glaciation. Additional

palynological studies have substantiated these earlier reports, and confirmed that a belt of fir (*Abies* sp.), hemlock (*Tsuga* sp.), and spruce (*Picea* sp.) existed across the central portion of the United States during maximum glaciation. Birch (*Betula* sp.), alder (*Alnus* sp.), and tamarack (*Larix* sp.) were present also. Sedges (*Cyperaceae*) and sagebrush (*Artemisia* sp.) were the main herb constituents of the boreal forest (Wright, 1970). Throughout the southern states, from northern Florida to Texas, boreal plant species were present but represented a more limited percentage of the total Pleistocene pollen-rain. For example, Hafsten (1964) noted that present-day grassland areas of west Texas were occupied by pine during late Wisconsin time. Recent studies (Watts and Wright, 1966; Kapp, 1970; Wright, 1970) suggested that in the Northern Great Plains, at least the Dakotas and portions of Kansas and Nebraska were occupied by a boreal spruce forest in Wisconsin time. Fossil spruce wood in glacial drift from Brookings County, South Dakota, has radiocarbon dates greater than 30,000 BP (Lemke *et al.*, 1965:21). The current latitudinal and altitudinal limits of spruce distribution approximate the 70°F July average isotherm (Kapp, 1970).

Braun (1951; 1955), Kendeigh (1961), and Thomas (1951) postulated a temperate biota inhabiting the margins of the glacier in the Great Lakes region and eastern North America, and argued for relatively little vegetational change south of the ice cap. In contrast, Cushing (1965) and Curtis (1959) favored an azonal mixed coniferous-deciduous vegetational margin south of the ice front. On the bases of pollen stratigraphy, periglacial geomorphology, plant macrofossils, and meteorological principles, other authors (Dillon, 1956; MacGinitie, 1959; Martin, 1959 and elsewhere; Guilday *et al.*, 1964; Bryson *et al.*, 1970) proposed vegetational zones of transition. These transitional zones progressed southward from apparently treeless tundra to boreal woodland, deciduous forest in the east or pine savanna and mixed gallery forest in the west, and finally to steppe or pine savanna farther south.

Pollen diagrams from artesian-spring marshes near Muscotah, Kansas, and from southern Minnesota provide no evidence of tundra bordering the ice sheet during the Full-glacial Period (Wright, 1970). However, pollen and plant macrofossils indicate a narrow zone of tundra did exist between the boreal forest and glacial front in northeastern Minnesota at a slightly later time (Watts, 1967).

The boreal flora evidently followed the glacier as it retreated northward in response to climatic change. Deteriorating spruce forest and the succeeding vegetation on the Great Plains varied from east to west corresponding to changes in moisture and from north to south in relation to temperature gradients and shifting isotherms.

The boreomontane character of the Black Hills was established during the Late-glacial times. This interval, which followed maximal advance of the Wisconsin glacial front, was a time of stagnation, retreat, and periodic minor readvance of the ice sheet. Presumably there was a general withdrawal of boreomontane elements from the Northern Great Plains, accompanied by an increasing invasion of temperate species. Disjunct populations of boreomontane mammals were left behind the retreating ice border in the Black Hills and in pockets of suitable sites across the plains.

Coincident with the northeastward retreat of the continental ice sheet, the boreal spruce forest may have spread over those parts of the Northern Great Plains that previously might have been treeless. The impressive cover of paleosols, sand dunes and loess (Peorian and Bignell) deposited over much of the region in late Pleistocene time opposes the hypothesis of a dense periglacial forest, at least northward from western Nebraska to the glacial border (Smith, 1965; Wright, 1970). Ecogeographic dis-

tributional patterns of steppe-related mammals also refute the presence of a dense woodland throughout the plains at this time (Hoffmann and Jones, 1970). Schultz *et al.* (1951:28) suggested that the formation of loess indicated a time of "reduced vegetative cover." In northeastern Kansas, the nature of the loess, the molluscan fauna of the loess, and the pollen diagrams from Muscotah indicate wooded environs. Farther west, the loess and associated molluscan fauna suggest a prairie environment interlaced with gallery forests that provided habitats for nongrassland species (Leonard and Frye, 1954). Kendeigh (1961) noted that the nature of the loess of the plains was indicative of grassland abutting directly against the glacial front. However, meteorological evidence suggests that grassland vegetation in the Northern Great Plains during the Late-glacial interval may have been restricted to the more arid rain shadows of the Rocky Mountains, in western Kansas and eastern Colorado (Bryson and Wendland, 1967).

Sand dunes are not well correlated with Pleistocene events, but the Bignell Loess is radiocarbon dated at about 12,600 BP (Watts and Wright, 1966), and maximum loess deposition occurred in Illinois and Iowa from 20,000 to 14,000 BP (Wright, 1970). Smith (1965) suggested that large transverse sand dunes were formed by periglacial winds from the north, at a time when unforested terrain could not interfere with dune development. Juxtaposition of the vast area of desertlike dunes in northern Nebraska in contrast to the well documented occurrence of a boreal spruce forest in other regions of the plains during Late-glacial time is compromised by Wright (1970). Retreat of the ice front, with subsequent decrease in velocity of periglacial winds, permitted the encroachment of vegetation that stabilized the dunes. Presence of the subalpine spruce forest in the Black Hills may indicate that boreal vegetation then spread rapidly over (or around) the Nebraska Sand Hills, eventually reaching the Black Hills.

Dillon (1956:173) mapped the hypothetical distribution of white spruce during Wisconsin time and suggested that boreal elements entered the Hills via a link with the Rocky Mountains. However, were this the case, the species in the Hills probably would be Engelmann's spruce (*Picea engelmanni*) (Halliday and Brown, 1943). Thus, the white spruce in the Black Hills seemingly was displaced originally from the Canadian or Hudsonian life-zones to the north. Evidence of coniferous species throughout South Dakota during some part of the late Pleistocene implies that boreal components could have invaded the Hills from several directions, following climatic change and resultant glacial retreat, rather than solely from the west. The present boreal elements in the Hills are disjunct from contiguous boreal forest, which is located some 435 miles to the north (Buttrick, 1914).

The cordilleran-montane biota also entered the Black Hills during the Full-glacial Period. Regional snow lines and montane biotic zones were depressed vertically about 4000-4500 feet during that time (Martin, 1959:394; Richmond, 1965:228; Webb, 1965:457). Richmond (*loc. cit.*) suggested a decrease of 16-17° F in summer temperature concurrent with the displacement. Coincident with these events, the cordilleran-montane elements extended considerably downslope, eastward and southward, invading the Black Hills, Laramie Mountains, and Great Plains along a wide front. Ensuing climatic changes during Late-glacial and Holocene times caused retreat of these components toward their previous centers, leaving relics in the Hills and other montane environs, on escarpments, and in favorable mesic sites on the plains. Montane floral elements of the Black Hills currently are disjunct from those to the west, the nearest populations residing in the Big Horn Mountains of Wyoming, about 150 miles distant.

Subsequent climatic oscillations were

not of equal direction or intensity. The chronology of climatic events depicted in Table 2 is based on episodes defined by Reid A. Bryson and others (Bryson and Wendland, 1967; Baerris and Bryson, 1965; Bryson *et al.*, 1970). More recent episodes have been further clarified by studies of cultural history (Lehmer, 1970) and of historical droughts (Tomanek and Hulett, 1970). Notations concerning biotic events follow Hoffmann and Jones (1970), Watts and Wright (1966), Wells (1970a, 1970b, 1970c), and Wright (1968, 1970).

Post-Wisconsin Events.—Climatic change that finally terminated the Pleistocene epoch brought about rapid phytogeographic change. On the eastern portion of the plains, spruce forest succumbed to a brief increase of alder and

TABLE 2.—Chronological events since maximal Wisconsin glaciation.

PLEISTOCENE EPOCH
Full-glacial Period (30,000 to 13,000 BP)—Maximum advance of Wisconsin ice sheet; summers moister and cooler, and winters warmer than present. Boreal spruce forest over much of Northern Great Plains; north-central Nebraska to glacial border presumably treeless; members of present plains biota occupy steppe and savannah conditions to south.
Late-glacial Period (13,000 to 10,500 BP)—Stagnation, retreat, and periodic minor readvance of ice sheet; culmination with Valders Readvance about 10,600 BP; summers moister and cooler, and winters warmer than present. Boreal forest still present; grassland restricted to arid rain shadow of Rocky Mountains; complex of steppe, taiga, and tundra biota in western section; pine savannah and steppe still south of Northern Great Plains.
HOLOCENE EPOCH
Pre-Boreal Period (10,500 to 9650 BP)—Shift in atmospheric circulation; retreat of ice sheet; low corridor opening between Arctic and Great Plains; frequent and intense polar storms; westerlies developing; increasingly continental climate with summers drier and warmer, but winters colder than present. Replacement of boreal forest by steppe on plains, and by deciduous elements to east.
Boreal Period (9650 to 8450 BP)—Increased frequency and strength of westerlies and polar storms; continental climate with summers drier and warmer, but winters colder than present. Spread of grassland northwestward south of ice front.
Atlantic Period (8450 to 4680 BP)—Increased southward flow of Arctic air; westerlies attain maximum strength; summers arid and warm, with increase in moisture late in period, but winters colder than present. Maximal eastward penetration of grassland; boreal and deciduous forest north of present limits.
Sub-Boreal Period (4680 to 2890 BP)—Southward shift of Arctic frontal zone; chinooks less frequent east of Rockies; temperatures cooler; climate similar to present by end of period. Steppes retreat to present limits; southward shift of boreal biota; lower tree line descent down eastern slopes of cordillera.
Sub-Atlantic Period (2890 to 1690 BP)—Shift in upper-air anticyclonic circulation; influx of tropical air resulting in moister climate than present. Possible influences on biota northeastward from Great Basin.
Scandic Period (1690 to 1100 BP)—Transition period back toward early Atlantic conditions, becoming warmer and drier once more.
Neo-Atlantic Period (1100 to 760 BP)—Subtropical anticyclones cause influx of moist tropical air; warmer climate continues. Conditions favorable for corn agriculture; horticultural villages established in Missouri River Valley.
Pacific Period (760 to 410 BP)—Increased westerlies across North America; resultant drier climate (30 to 50 percent decrease in summer precipitation); return to Neo-Atlantic conditions later in period. Decreased extent of occupation of Missouri River Valley by village tribes; return of occupancy later in period.
Neo-Boreal Period (410 to 115 BP)—Westerlies and polar storm tracks shift southward and intensify; summers drier and cooler; increased moisture later in period. Small temporary villages with marginal economy in Missouri River Valley; larger more permanent villages later in period; effects of European man after 290 BP.
Recent Period (115 to present)—Increased westerlies resulting in warm, semiarid climate at present; short periods of drought commencing about 102, 91, 60, and 18 BP.

birch, which in turn were replaced by other temperate deciduous elements such as elm (*Ulmus* sp.), hop hornbeam, hazel (*Corylus* sp.), and oak (*Quercus* sp.), with parklike openings inhabited by herbs and grasses (Watts and Bright, 1968; Wright, 1970). To the west in Kansas, Nebraska, and the Dakotas, the boreal forest gave way directly to prairie species (Wright, 1968, 1970). Two records of tundra-related mammals noted for South Dakota suggest an environment equivalent to present day Hudsonian and Canadian life-zones. Martin (1959:398) reported a muskox (questionably *Ovibos*) with a radiocarbon date of 9700± 600 BP, and Green and Lilligraven (1965:48) listed a fossil caribou from the late Pleistocene in Gregory County. Relict populations of boreal and montane species of plants and animals on the Black Hills also attest to these environmental conditions (Jones, 1964:21).

Time of demise of the boreal spruce forest in the plains region has been recorded by various authors, as follows: Muscotah, in northwestern Kansas, 15,880-11,340 BP (Wright, 1970); Rosebud, in the Sand Hills near the Nebraska-South Dakota state line, 12,600 BP (Watts and Wright, 1966); Rosebud in western Kansas and Nebraska, 11,400-9100 BP (Ruhe, 1970); Pickerel Lake, in northeastern South Dakota, 10,670 BP (Watts and Bright, 1968); Pickerel Lake in Iowa, 8000-7000 BP (Ruhe, 1970). The tree-prairie transition is dated by Wright (1970) at 12,000 BP in the southern portion of the Great Plains and 9500 BP in the northern section.

Later occurrence (5040 BP) of woodlands (with somewhat more pine than present today) on the plains of north-central Nebraska and South Dakota is well documented also (Kapp, 1970; Sears, 1961; Watts and Wright, 1966; Wright, 1970). Wells (1970b) recorded the mid-post-glacial flora of the Laramie Basin, southwest of the Black Hills, as being an open xerophilous woodland dominated by western red cedar and ponderosa pine with lower synusia of semidesert shrubs and grasses.

The available evidence suggests a more or less azonal plant and animal community similar to that postulated by Jones (1964:23) for Nebraska during maximal glaciation in the Northern Great Plains during Late-glacial and early post-glacial times. Both prairie and forest components may have occurred in the same general area to form a savanna-like landscape. The relative frequency of boreal elements decreased from north to south and deciduous elements decreased from east to west. Relatively cold-tolerant, widely distributed temperate species of grassland affinity may have been segregated ecologically in accordance with local conditions (Jones, *loc. cit.*). The supposition of an admixture of northern and southern elements in the plains region also is in agreement with the viewpoint of Smith (1957:207).

During warm, relatively moist intervals of post-glacial time, such as in the Sub-Atlantic or Neo-Atlantic periods, elements of the eastern deciduous forest and tall-grass prairie biotas probably extended westward far onto the plains (eastern deciduous species via mesic gallery forests along river systems and valleys, and tall-grass components on the uplands). Hardier boreal elements remaining from the Late-glacial Period presumably could have survived these somewhat mild climatic conditions in comparatively undisturbed, disjunct populations. Jones (1964) interpreted the relatively large amount of fossil pine pollen described from the Nebraska Sand Hills by Sears (1961) to indicate that boreal species survived early post-glacial time only to be excluded by ensuing mid-post-glacial periods of maximum warmth and dryness. The eastern deciduous biota may have mingled with residual cordilleran elements (from Pleistocene or Sub-Boreal times when the biota spread eastward and southward down the slopes of the cordillera) at points throughout the Great Plains (Webb, 1965).

Conversely, arid post-glacial periods

were a time of extirpation of the boreal and cordilleran-montane elements that survived from late Pleistocene time on the Northern Plains; only the most tolerant species survived in small, isolated populations. Much of the unique biota of the Black Hills may have been restricted during these periods. Outlying representatives probably could not survive the effects of the hot, dry climate; the milder, more stable climate in the Black Hills presumably afforded a suitable refugium for these elements. Those species of eastern and southern affinities that had spread into the Northern Great Plains area during the humid climatic episodes either found suitable refugia during the time of evapotranspirative stress, or were subsequently excluded.

During the mid-post-glacial time of maximal aridity, xeric plant species supplanted mesophytic vegetation; these species fragmented formerly continuous areas of deciduous vegetation and permitted encroachment of arid-tolerant trees and nonarboreal plants (Smith, 1965). Gleason (1923) invoked an eastward extension of the prairie to explain the relict pattern of prairie plant distribution (prairie peninsula) in the Midwest, and postulated the extension prior to the invasion of deciduous species in post-glacial time. Transeau (1935) indicated that the extension was subsequent to the initial invasion of the deciduous forest in mid-post-glacial time. Available evidence implies that maximal eastward penetration of the grassland occurred in the Atlantic Period. However, as with the north-south glacial displacement of the biota, the west to east dispersal of prairie species may have been repeated several times.

Thus, during milder intervals of post-glacial time, species having eastern and possibly southern affinities spread onto the Northern Great Plains and Black Hills, and mixed with residual boreal and cordilleran-montane constituents. During subsequent arid climatic episodes, these immigrants either inhabited suitable refugia or were eliminated when drought environment promoted an eastward expansion of the steppes. In time, amelioration of dry conditions resulted in retreat of grasslands to their present limits. This sequential series of events can be traced in pollen diagrams of Pickerel Lake and Muscotah (Watts and Bright, 1968; Wright, 1970). Wells (1970b) described the present flora of the Laramie Basin as desertic in physiognomy with strong resemblance to winter-cold deserts of the Great Basin and Colorado Plateau. Change from a xerophilous woodland to a semidesert shrubland in post-glacial time denotes a secular trend toward an increasingly arid climate east of the Laramie Front Range. Recession of the boreal forest barrier that existed between the Great Basin and Wyoming Basin during the Wisconsin (Hoffmann and Jones, 1970) opened access for cold-desert species to the Northern Great Plains. Shifts in upper-air anticyclonic circulation northeastward from the Great Basin in the Sub-Atlantic and resultant influx of tropical air also may have influenced the biota of the region. For example, evidence of extensive introgression between the bur oak in the Black Hills and Gambel's oak (*Quercus gambelii*) to the southwest, in the central Rocky Mountains, presupposes a massive northeastward migration of the cold-intolerant Gambel's oak during a warm moist period (Wells, 1970b). Such conditions were not current during eastward and southward displacements of cordilleran-montane elements.

The sequence of episodes in the history of native cultures of the Missouri River Valley in the Dakotas (Lehmer, 1970) and the Mill Creek culture of Iowa (Bryson *et al.*, 1970) implies a close correlation between climatic and cultural changes in near-modern time. Moderation, culminating in the present climatic conditions, has been interrupted by a gradual warming trend on the North American continent in the last 100 years (Dorf, 1959, and others). Periodic, extended droughts have resulted in changes of the grasslands and associated fauna

(Tomanek and Hulett, 1970). Wooster (1935, 1939) and Gier (1967) noted that some mammals, such as the prairie vole (*Microtus ochrogaster*), almost disappear in some areas under arid regimes, whereas others, such as the deer mouse (*Peromyscus maniculatus*), seem relatively unaffected by extended drought.

The Great Plains of Recent time is an extensive grassland on deep, transported soils, corresponding to flat or gently rolling topography. The graminoid flora is defined by a predominance of a few widespread species and a paucity of endemics, virtually none of which are grasses (Wells, 1970c). The associated insect fauna (e.g., range grasshoppers and lataline grass-feeding leafhoppers), has similar distributional characteristics; however, the fauna has a much greater species diversity in certain seral stages of surrounding forested biomes than in comparable grassland communities (Ross, 1970). Generally, trees are restricted to riparian habitats as gallery forests along water courses; in addition, nonriparian woodlands occur on escarpments and other topographic breaks throughout the grassland province of central North America.

Clements and Chaney (1937) indicated that the prairie species probably developed after Miocene time in the central parts of the continental United States due to drier conditions created by mountain building to the west. However, Wells (1965, 1970a, 1970b, 1970c) and Ross (1970) presented several arguments for relatively recent tenure of the central grasslands. Accumulated evidence indicates that these extensive treeless steppes probably have not had a continuous existence since the mid-Tertiary. The abundant, nonarboreal pollen reported by Kapp (1970) from interglacial sediments of the Sangamon interval may be from restricted refugia; the occurrence of the pollen does not necessarily imply the presence of widely distributed steppe vegetation. During maximal Wisconsin glaciation, grassland species survived in suitable refugia southwest and southeast of the glacial front or possibly as mosaic distributions in a prairie-forest savanna. When one realizes that most grassland species have a major part of their diverse ranges as synusial components of seral stages of forested environs, the uniqueness of the prairie biome begins to fade; consequently, the grasslands should be regarded as consisting of a derivative biota.

Climate alone does not account for a grassland climax vegetation. In areas where grasslands were planted in Nebraska with upland tree species native to scarp woodlands, rather extensive forest became established (Wells, 1965). Furthermore, Potter and Green (1964: 22) found evidence of ponderosa pine, as seedlings and young saplings, invading the grasslands in North Dakota. A similar invasion can be observed on the prairie of Wind Cave National Park, where grazing by bison checks the reproduction of ponderosa pine. Thus, in at least certain locations, the plains are quite capable of supporting nonriparian woodlands (at least of xerophytic conifers). Physiography may be as important a factor as climate in affecting the distribution of extensive, treeless grasslands.

Stewart (1951) noted that theoretical climatic climax vegetation in savanna and grassland areas probably postdates the arrival of man. The Tule Spring, Nevada site, dated at +23,000 BP, clearly indicates that prehistoric man was present during maximum glaciation in the Wisconsin (Martin, 1958). The frequency of fires, which generally is assumed to have increased with the arrival of man, is well documented in early historical literature. Scarps and abrupt topographic breaks may have served as refugia from grass fires for the nonriparian woodlands of the plains region (Wells, 1965, 1970a, 1970b, 1970c).

Forest fires may have terminated broad expanses of boreal forest that were already suffering evapotranspirative stress from the effects of warm postglacial climate. These newly opened

expanses subsequently were invaded by a biota having strong ecological affinities with nearby forested biomes. Interaction of topography, climate, and subsequent prairie fires apparently has resulted in the present physiognomy of the Northern Great Plains. See the several papers of Wells cited above for additional arguments concerning these points.

The introduction and development of modern civilization and agriculture in the plains region no doubt have resulted in extirpation of several species, endangered others, and caused widespread, drastic modification of habitats that fragmented the ranges of yet other species (Smith, 1965). In addition, man has introduced many exotics (e.g., Kentucky bluegrass) and thereby possibly caused the exclusion of native species or shifts in their respective ranges.

The Black Hills flora is diverse, with many species occupying a small geographical area. For example, Froiland (1962) identified 20 kinds of willows (*Salix* sp.) of diverse geographic origin in the Hills region. This diversity is due partly to the varied topography and habitats available, and partly to the past movement of great floral assemblages during late Tertiary and early Pleistocene times (Wetmore, 1968). However, the Black Hills are not unique in having distributional limits of so many northern, southern, eastern and western species.

The probable geographic origin of the vegetative components of the Black Hills are listed in Tables 3 and 4. The presence of many widespread species (22-34%) can be attributed to the fact that plants with wide ranges of tolerance overlap distributionally within the Hills region. Most northern or boreal (6%) and western or montane (25-30%) species were displaced southward or eastward by advance of continental and Cordilleran ice sheets, respectively. These species became stranded on the Hills by migrating up the slopes after glacial retreat; although many species presumably were extirpated in the Atlantic Period, some remain currently.

Table 3.—Distributional patterns of the flora of the Black Hills, as noted by Hayward (1928) and McIntoch (1931).

Biographic origin	Percent affinity
Western	25–30
Widespread	22–34
Great Plains	17–26
Eastern	9
Northern	6
Southern	4–5

Table 4.—Distributional patterns of lichens of the Black Hills as noted by Wetmore (1968).

Biogeographic origin	Percent affinity
Arctic-Boreal	44.4
Pan Boreal	24.9
Pan Temperate	5.4
Western Temperate	4.9
Arid Southwestern	4.4
Pan North America	3.9
Southern Rockies-Alleghenian-Great Lakes	3.9
Eastern Temperate	3.4
Eastern Boreal	2.9
Grassland	1.5
Western Boreal	0.5

Examples of boreal species are paper birch, twin-flower, Venus' slipper, bunchberry, squashberry, and white spruce. Montane species include Oregon grape, Indian paint-brush, mariposa lily, skunkbush sumac, buffaloberry, white spruce and ponderosa pine. Fernald (1935) suggested that a few western species—for example, gland stem and huckleberry—may represent pre-Pleistocene floral elements.

Great Plains components (17-26%) are to be expected because of the location of the Black Hills, which are entirely surrounded by plains. These plants are found in the foothills, in the drier meadows, and open parklands. Examples are blue grama, Indian grass, porcupine grass, and western sandcherry. Eastern species (9%) presumably reached the Hills during the Sub-Atlantic or Neo-Atlantic intervals via gallery forests along water courses and uplands. These may be Ozarkian and Alleghenian elements of the eastern deciduous forest (Braun,

1947). Examples are hop hornbeam, American elm, boxelder, Solomon's seal, green ash, and bur oak.

The southern components (4-5%) probably arrived at about the same time as did the eastern elements. In part these are derived from the old Madro-Tertiary flora that developed in the southwestern United States in Miocene, Oligocene, and Pliocene times (Wetmore, 1968). The driest areas of the foothills now are occupied by the following species: soapweed, brittle pricklypear cactus, skunkweed, scarlet gaura, silver sagebrush, and wormwood. The examples used in this resumé were taken from Wetmore (1968).

The distributions of lichens in the Black Hills are vastly more complex than the respective distributions of vascular plants because of the diversity of substrates, exposed geological materials, elevations and relief, climatic range, and vegetational types. The probable geographic origins of the lichens in the Black Hills are listed in Table 4. For a thorough analysis of the complexities involved in distributional patterns of lichens, see Wetmore (1968).

INFLUENCE OF MAN ON THE ENVIRONMENT

The Black Hills region is one of the most densely populated areas of the Great Plains. In 1960, the Hills area contained an average of 6.2 persons per square mile. Of the native population, 57 percent were classified as urban, 30 percent as nonfarm rural, and 13 percent as farm rural. The presence of about 6000 armed forces personnel and from four to five million annual tourists intensifies utilization of Black Hills environments.

Changes wrought by man have been detrimental to some mammalian species and advantageous to others. Large herbivores and carnivores, such as the bison and wolf (*Canis lupus*), have been directly extirpated by man; populations of other species such as the mountain lion (*Felis concolor*), black bear (*Ursus americanus*), and prairie dog, have been reduced drastically. When European man first moved into the Black Hills, big-game mammals, fur-bearing mammals, and smaller game mammals were abundant, but subsequently they have become the object of exploitation. As agricultural endeavors in the region increased, carnivores and rodents were poisoned indiscriminately. Fortunately, recent programs of wildlife management and a more intelligent application of rodent and predator control have lessened the devastation by man. Establishment of Wind Cave National Park, Custer State Park, and several other areas has served to protect and preserve remnants of the native fauna. Man has reintroduced several species that formerly were native to the Black Hills, such as the elk (*Cervus canadensis*), pronghorn, bison, and mountain sheep. In addition, the mountain goat, fox squirrel (*Sciurus niger*), house mouse (*Mus musculus*), and Norway rat (*Rattus norvegicus*), which are not native to the Hills, were introduced by man. Activities of man that have indirectly affected the abundance and distribution of mammalian species in the Black Hills are summarized below. For detailed information concerning these activities, the reader is directed to the "Black Hills Area Resource Study," published jointly by the Departments of Agriculture and the Interior in February 1967.

Mining.—The gold rush of 1874-79 gave impetus to the mining industry in the Black Hills region. In the early 1900's, mining of silver, tin, coal, and crude oil flourished. The two World Wars created a greater demand for various minerals and gave added impetus to the tungsten, sheet mica, feldspar, bentonite, beryl, and lithium industries in the Hills. The most recent mining boom began in 1951, with the discovery of uranium ores in Jurassic-Cretaceous sandstones. Production of nonmetallic commodities, such as sand, gravel, crushed rock, cement, and clay, also are current industries of the region. Mining

invariably alters the natural environment. For example, in processing bentonite, the overburden is stripped off and the bentonite is turned over and stored in place for long periods of time. Excavation of mining complexes and rock quarries also has altered the topography. Processing of gold in the Lead-Deadwood area has resulted in pollution of many nearby streams. However, not all alterations have been detrimental to the regional fauna; for example, mines frequently are utilized by woodrats and various species of bats.

Timbering.—Cutting of timber commenced simultaneously with the Black Hills gold rush, and at least two portable, steampowered sawmills existed in the Hills by 1877. Intensive timbering caused a rapid depreciation of the quality in native stands adjacent to mining operations by 1897, when President Cleveland created the Black Hills National Forest Reserve. Sale of federal timber was authorized by the Timber Reserve Bill, enacted later in the same year. The timber industry developed rapidly, supplying vast quantities of wood products to the mines, railroads, and other industries of the region. The pulp and paper, and the post and pole industries have flourished recently. Forest production accounts for about 14.7 percent of the principal land use in the Black Hills. The total of commercial timber currently available in the Hills is estimated at five billion board feet; production in 1964 was in excess of 21.8 million cubic feet, contributing 6.5 million dollars to the regional economy. Exploitation of forests by lumbering is evidenced by vast areas of scrubby second-growth timber and numerous open areas where burning has resulted from lumbering operations. Removal of dead trees in clearing operations has eliminated potential den sites for flying squirrels and red squirrels. However, populations of some mammals (e.g., deer and chipmunks) have increased in areas of stumps, logs and trimmings.

Agriculture.—Homesteaders first moved into the Black Hills about 1900, but the drought of 1910-11 shifted major emphasis from general farming to the raising of livestock. Ranching became an important activity in the unforested uplands, foothills, and the Red Valley. Grazing now accounts for 75.1 percent of the principal land use in the Black Hills area; usually beef cattle and sheep are marketed as feeder stock.

About 103,000 acres were under irrigation in the Hills region in 1960. Cropland comprises about 8.6 percent of the principal land use, with corn, sorghum, winter wheat, spring wheat, barley, alfalfa, and hay being the major dryland crops. The average farm in the Hills area in 1960 was 2550 acres in extent, and sales of agricultural products amounted to more than 50 million dollars. The environment has been modified conspicuously due to agricultural practices. The original prairie grasslands of the Red Valley have been altered by grazing and the upland grasslands (e.g., the Reynolds and Gillette prairies) now support hayfields, market gardens, and pastures. Wind Cave National Park is one of the few large areas wherein native prairie grassland still exists nearly in its original state.

Fires.—The earliest records of fire in the Black Hills were about 1730 to 1740, when the entire area appears to have burned by a series of fires; in the period between 1790 and 1800, most of the Hills were burned again (Graves, 1899). Lesser fires of considerable extent occurred in 1842, 1852, and 1875. From 1880 through 1966, at least 70 fires in the Black Hills burned more than 175,000 acres of forest and grassland. Of these, 44 percent were known to have been caused by man and 18 percent by lightning, whereas 38 percent were of unknown cause (records of U. S. Forest Service, Black Hills National Forest). Among the more notable fires were those of Iron Creek in 1899 (38,000 acres), Rochford in 1931 (21,640 acres), McVey in 1939 (21,875 acres), and Wildcat in

1960 (10,336 acres). Improved precautionary measures and modern fire-fighting techniques have prevented major fires in recent years. Two smaller fires should be mentioned. Although the Deadwood fire burned only 4501 acres, it forced evacuation of that historic town in 1959. The Headquarters fire in Wind Cave National Park in 1964 (4000 acres) greatly endangered the native wildlife in the Park. A noticeable result of forest fires is the opening of extensive new grassland, and the establishment of aspen and birch woodlands in burned areas. Reforestation programs and natural secondary regeneration have partially revegetated the scarred hillsides that resulted from past fires.

Recreation and Tourism.—Although immeasurable in extent, perhaps the most detrimental influence on the environment of the Black Hills in the past few decades has been the influx of four to five million tourists annually. These visitors have intruded into canyons, onto the forested slopes, and upon much of the remainder of the relatively undisturbed environment in countless ways. Recreation and tourism are the foremost producers of revenue in the Black Hills; more than 120 million dollars were contributed to the regional economy by this industry in 1966. People seeking recreation are attracted to the Black Hills by points of historic and geologic interest, by opportunities to hunt and fish, and by such scenic features as Custer State Park, Wind Cave National Park, Jewel Cave National Monument, Devils Tower National Monument, and Mount Rushmore National Memorial. Demands for recreation surely will continue to increase in the future, as will exploitation of the once pristine environment.

ACCOUNTS OF SPECIES

ORDER INSECTIVORA—Insectivores

Family SORICIDAE—Shrews

In the Black Hills, the order Insectivora is represented by one species of the genus *Sorex*. An additional species of this genus may occur in the Hills, and another has been incorrectly reported from the area.

Sorex cinereus haydeni Baird

Masked Shrew

Sorex haydeni Baird, 1858, Mammals, *in* Reports of explorations and surveys . . . from the Mississippi River to the Pacific Ocean . . ., 8 (1):29, 14 July (type locality restricted to Fort Union, just west of confluence of Missouri and Yellowstone rivers, Williams Co., North Dakota, by Merriam, N. Amer. Fauna, 10:60, 31 December 1895).

Sorex cinereus haydeni—Jackson, 1925, Jour. Mamm., 6:56, 9 February.

Vernon Bailey (1888:436) first reported the masked shrew from the Black Hills under the name *Sorex personatus*. Known altitudinal range in the Hills extends from 4500 to 6500 feet, but this shrew is most widely distributed in the Central Basin and on the Limestone Plateau above 5500 feet. It is common locally in riparian associations and other moist habitats throughout the Northern Great Plains. Except for three individuals obtained in October and November, all specimens examined were taken in warm months.

In the Hills, this species is most numerous in montane habitats; it is locally abundant in marshy areas, mossy bogs, and other riparian associations of grasses, sedges, rushes, aspen, birch, and willow. Many specimens were trapped near logs, large rocks, or low shrubs located in dense grass along creeks such as Beaver, Boxelder, Castle, Cold, Grizzly, Iron, Rapid, Rattlesnake, Spring, and Willow, or in the vicinity of beaver dams. Spring-fed bogs and other moist areas in aspen and spruce woodlands also provide suitable habitat for these shrews.

The availability of ground water undoubtedly is one of the most important factors limiting the distribution of *S. c. haydeni*. A few individuals have been taken in unusual habitats; for example,

a female was trapped on a rock ledge near the top of a 30-foot cliff, and four others were obtained on dry, rocky, pine-clad hillsides approximately 200 feet from the nearest source of water. Also, two shrews taken by Bailey (1888:436) were captured "at holes in the rocks on top of one of the highest peaks." Population densities frequently are low in these marginal areas. Associated with the masked shrew in moist habitats are *Zapus hudsonius, Microtus longicaudus,* and *M. pennsylvanicus. Peromyscus maniculatus, Clethrionomys gapperi,* and *Eutamias minimus* have been taken with these insectivores in drier environments.

A member of a University of Kansas field party, J. R. Choate, buried 20 cans in tall grass along Boxelder Creek, 20 mi. W Nemo between 29 June and 5 July 1967. The cans were buried 10 paces apart with the openings at ground level. A snap-trap was placed within five feet of each can. These pitfalls (three shrews captured) seemed to be a more efficient method of obtaining S. *c. haydeni* than was snap-trapping (one shrew captured); however, these data are insufficient and a more thorough application of this technique in the Hills region is desirable. Trapped insects may have attracted the shrews to the pitfalls.

Reproductive data are available for S. *c. haydeni* in the Black Hills from mid-June through mid-July. Of 33 females captured during this period, 15 showed no sign of reproductive activity; the same was true for a female taken in Spearfish Canyon on 7 August. Mammae of a female obtained on 18 June were enlarged, whereas another captured on 24 June had an enlarged uterus, possibly indicating recent implantation. Twelve females taken in the period 25 June to 7 July carried 5.2 (2-7) embryos that were 5.9 (2-11) in crown-rump length. Four lactating females were noted in the period 27 June to 13 July. The testes of 14 males captured early in the summer were 4.5 (2-6) in length, whereas those of three taken early in August were 3. Pruitt (1954:36) reported that reproduction occurs only in fully matured or old individuals in S. *c. cinereus* in Michigan. Three young females of age class two of Pruitt (*loc. cit.*) were obtained in summer and were gravid; these were taken on 25 June (seven embryos), 29 June (five embryos) and 2 July (five embryos). Pruitt also indicated that the testes of reproductively active males exceeded two millimeters in length; testicular length of an immature male obtained on 3 July was 5. While uncommon, such precocious reproductive activity has been reported in other species of the genus *Sorex.* Young of the year were evident from late June through mid-August.

Due to the uniformity in season of collection (mid-June to early August), most of the specimens examined were in summer pelage. However, a male obtained by Vernon Bailey near Sundance on 13 August 1913 evidenced molt, with fresh winter pelage covering about two-thirds of both dorsum and venter; three others, taken by Merritt Cary in the Bear Lodge Mountains on 22 June 1912, had just completed molt.

In considering geographic variation, specimens of S. *c. haydeni* from the Black Hills were compared with individuals from south-central Wyoming (Albany and Carbon counties), North Dakota (Bowman and Walsh counties), eastern South Dakota (Kingsbury, Union, Marshall and Day counties), and northern Nebraska (Sioux, Sheridan, Cherry, and Keya Paha counties). Cranial measurements were taken in the manner described by Jackson (1928:12) and Findley (1955:5). Cranial breadths of 29 females averaged somewhat greater (7.8 ± 0.21) than those of 22 males (7.6 ± 0.22). Otherwise, significant secondary sexual differences were not apparent nor was significant variation within the Hills population detectable.

Reflectance readings show that masked shrews vary geographically in tone of color. Individuals from North Dakota and north-central Wyoming averaged paler than those from the Black Hills, whereas specimens from south-

central Wyoming and Nebraska averaged darker than Hills specimens. Shrews from eastern South Dakota approached those from the Hills in coloration (Table 5). No significant geographical differences in hue were discernible.

Both external and cranial dimensions evince considerable geographic variation. Masked shrews from localities west of the Black Hills have greater average body, tail, maxillary tooth-row, and palate lengths, as noted by Long (1965: 519). However, these individuals are indistinguishable from eastern representatives on the basis of condylobasal length and interorbital breadth. In addition, the average rostral length is greater and the breadth across the maxillary processes is significantly less than noted in specimens from sites east of the Black Hills. I am in agreement with Long (*loc. cit.*), who assigned masked shrews from northeastern Wyoming to *S. c. haydeni* and those from elsewhere in that state to *S. c. cinereus*. In most dimensions, specimens from the Black Hills are intermediate between *S. c. cinereus* to the west in Wyoming and *S. c. haydeni* to the east in the Dakotas and Nebraska, but fall within the range of variation of the eastern specimens and hence are assigned to *S. c. haydeni*. Additional measurements (not listed in table 5) of 67 adult shrews from the Black Hills are: percent red reflectance, 54.3±0.52; percent green reflectance, 23.7±0.19; percent blue reflectance, 21.3±0.32; hind foot length, 11.2±0.64; ear length, 6.4±1.25; weight, 3.9±0.94; condylobasal length, 15.5±0.28; cranial breadth, 7.7±0.23; interorbital constriction, 2.8±0.11; skull depth, 4.7±0.33.

Specimens examined (136).—SOUTH DAKOTA: *Lawrence County:* Deadwood, 3 (USNM); Dumont, 6100 ft, 3 (USNM); 2 mi S Tinton, 6100 ft, 6; Big Spearfish Canyon, 9 mi S, 3 mi W Spearfish, 5000 ft, 2; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 2; 3 mi W Nemo, 4800 ft, 2; 2 mi W Nemo, 4700 ft, 20; Nemo, 4700 ft, 1. *Pennington County:* 3 mi W Rapid City, 1; 20 mi N Elk Mountain, 1 (USNM); Moon, 22 mi W Hill

Table 5.—Geographic variation in selected color, and external and cranial measurements of adult *Sorex cinereus* from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Total length	Tail length	Rostral length	Maxillary breadth	Palatal length	Length of maxillary tooth-row
4 (2♂, 2♀)			*S. c. haydeni*, North Dakota				
Mean	28.0	86.0	35.0	5.1	4.3	6.0	5.4
SD	±4.24	±5.66	±0.00	±0.07	±0.14	±0.14	±0.21
7 (5♂, 2♀)			*S. c. haydeni*, eastern South Dakota				
Mean	20.4	87.3	33.0	5.3	4.2	6.1	5.5
SD	±5.08	±1.86	±2.45	±0.15	±0.18	±0.07	±0.09
13 (6♂, 7♀)			*S. c. haydeni*, northern Nebraska				
Mean	16.8	91.8	33.5	5.3	4.2	6.1	5.6
SD	±2.55	±3.77	±2.29	±0.12	±0.11	±0.13	±0.13
67 (30♂, 37♀)			*S. c. haydeni*, Black Hills, South Dakota and Wyoming				
Mean	19.6	92.3	37.2	5.3	4.2	6.2	5.6
SD	±2.95	±5.14	±3.30	±0.14	±0.11	±0.16	±0.14
20 (9♂, 11♀)			*S. c. cinereus*, north-central Wyoming				
Mean	22.9	93.3	37.1	5.4	4.1	6.3	5.7
SD	±3.12	±5.54	±2.16	±0.12	±0.10	±0.16	±0.14
73 (44♂, 29♀)			*S. c. cinereus*, south-central Wyoming				
Mean	19.0	96.3	38.8	5.4	4.1	6.2	5.6
SD	±2.75	±5.50	±2.50	±0.15	±0.13	±0.16	±0.13

City, 6200 ft, 1; Ditch Creek, 14 mi W Hill City, 6400 ft, 1; Palmer Gulch, 3 mi SE Hill City, 53-5400 ft, 16 (UMMZ); 3 mi SSE Hill City, 1 (UMMZ); Willow Creek, 4 mi SE Hill City, 53-5400 ft, 12 (UMMZ); Castle Creek, 6500 ft, 3 (UMMZ); Spring Creek, 2 mi W Oreville, 5500 ft, 3 (UMMZ); Rapid Creek, 1.5 mi W Rochford, 1 (UMMZ); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 6; 3 mi N, 7 mi W Deerfield, 6400 ft, 1; 3 mi S, 1 mi W Rockerville, 1; 16 mi NW Custer, 1 (UMMZ). *Custer County:* 0.5 mi E Sylvan Lake, 6250 ft, 2 (UMMZ); 5.75 mi N, 5.75 mi E Custer, 5220 ft, 19; 16 mi W Custer, 2 (USNM); Custer, 3 (2 USNM, 1 AMNH); Lightning Creek, 8 mi SW Custer, 5100 ft, 1 (UMMZ).

WYOMING: *Crook County:* Beaver Creek, Bear Lodge Mountains, 6.5 mi SSE Alva, 1 (UMMZ); Warren Peak, Bear Lodge Mountains, 6000 ft, 4 (USNM); Sundance, 3 (USNM); Rattlesnake Creek, 6000 ft, 1 (USNM); 3 mi NW Sundance, 5900 ft, 10. *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 2.

Additional records.—SOUTH DAKOTA: *Lawrence County:* Spearfish (USBS files); Rochford (USBS files). *Custer County:* Bull Springs, 2 mi N, 9 mi W Custer (Bole and Moulthrop, 1942:95). *County unspecified:* Black Hills (Bailey, 1888:436).

ORDER CHIROPTERA—Bats

Family VESPERTILIONIDAE—Vespertilionids

Ten species of bats, representing five genera, are known to occur in the Black Hills of South Dakota and Wyoming. One additional species of another genus (*Euderma*) is unreported as yet, but may inhabit the area; another species has been erroneously reported from the Hills and the status of still another remains uncertain. Chiropterans from the Black Hills represent but one family, Vespertilionidae, in the suborder Microchiroptera. Three species are known to migrate southward during the colder months, whereas six are resident year-round in the area; the seasonal distribution of one species (*Myotis keenii*) is in question.

The Black Hills contain a large number of potentially favorable retreats for many kinds of bats. The mountainous terrain is comprised of uplifted segments of granite, and exposed cliffs and rock ledges of limestone and sandstone. Huge caverns and lesser caves have formed naturally in the soluble limestone layers. Jewel Cave, Wind Cave, Davenport Cave, Ice Cave, Bear Trap Cave, Igloo Cave, and the numerous unnamed and/or commercial caves of the region serve as hibernacula in the colder months. Mining in the Hills began with the gold rush of the mid-1870's. Mica, silver, tin, coal, tungsten, and uranium mining flourished in later periods. As a consequence, old mine shafts and tunnels are available for utilization by bats. Also, the mature ponderosa pine forest, and the numerous deserted farm buildings and mining shanties serve as roosting sites for those species preferring these habitations.

Jones and Genoways (1967b:184-196) summarized the distributional status of bats in South Dakota on the basis of data accumulated prior to 1967. Subsequently, additional observations on bats from western South Dakota (Turner and Jones, 1968:444-447) and the Black Hills (Turner and Davis, 1970:360-364) have been published. In the following accounts, pertinent data are summarized or cross-referenced in an effort to avoid repetition. Robert A. Martin, South Dakota School of Mines and Technology, Rapid City, currently is studying several aspects of bat biology in the Black Hills.

Myotis keenii septentrionalis (Trouessart)

Keen's Myotis

[*Vespertilio gryphus*] *var. septentrionalis* Trouessart, 1897, Catalogus mammalium . . ., fasc. 1, p. 131 (type locality, Halifax, Nova Scotia).

Myotis keenii septentrionalis—Miller and G. M. Allen, 1928, Bull. U. S. Nat. Mus., 144:105, 25 May.

Keen's myotis is known in the Black Hills from Pennington and Custer counties in South Dakota, and from Weston County, in Wyoming. The species was first reported from the area by Miller and Allen (1928:107) from Elk Mountain, Custer County. Its distribution and systematics subsequently were summarized by Jones and Genoways (1967b:185).

In the summer of 1968, field work in the Hills area revealed Keen's myotis to

be common locally (Turner and Davis, 1970:360), although previously this species had been considered to be rare. Eight males were taken in a mist net set within the entrance to Jewel Cave on 24 July (see account of *M. lucifugus*). Eight males and one female were netted at the entrance to Ice Cave on 26 July (see account of *M. thysanodes*), and five males and one female were captured in nets set over two small ponds near Moon on 30 July. An additional female was netted over one of these ponds on 20 August (see account of *L. borealis*). Extensive use of mist nets, rather than shooting at dusk, undoubtedly contributed to increased success in capturing this bat. At one place or another, all nine other species of bats in the Hills have been netted in company with Keen's myotis.

The status of *M. keenii* in the Black Hills in winter months remains uncertain. Specimens have been taken in the area from 9 June through 25 August. R. A. Martin (pers. com.) investigated more than 100 caves and mine shafts in Lawrence, Pennington, and Custer counties in the winter of 1969-70, but *M. keenii* was not observed in any of these hibernacula. Presumably the species represents a disjunct population in the Black Hills region; the nearest localities of record are 252 miles to the north at Fort Buford, Williams Co., North Dakota (Miller and Allen, 1928:106-107), and 296 miles to the southeast at a locality 3 mi SW Springfield, Bon Homme Co., South Dakota (Jones and Genoways, 1967b:185). Surely, if this species of bat were a transient, it would be in evidence along routes of migration. Thus, based on distributional data, the species is assumed to be resident in the Hills throughout the year.

Ecological information pertinent to *M. keenii* in the Black Hills is limited. Known altitudinal range is between 4000 and 6500 feet. Three specimens collected on 19 July 1951 near Buckhorn, Weston Co., Wyoming, were found roosting in old buildings of a sawmill. A foraging male was shot about 8:30 P.M. (MDT) on 9 June 1965 over Porcupine Draw; this individual was found with two *M. lucifugus*, one *M. leibii*, 11 *M. volans*, and one *Lasiurus cinereus*. Procupine Draw enters Ditch Creek Valley from the east; its steep rocky hillsides are clad in ponderosa pine and white spruce.

A single, lactating female was obtained in Ice Cave on 26 July; two other lactating females were taken near Moon on 30 July and 20 August. A subadult male (evidenced by unfused phalangeal epiphyses) was captured at Ice Cave on 26 July. The testes of a male shot in early June were 2 in length, whereas those of 21 males collected in late July had an average length of 4.8 (3-6). Molt was underway on 10 males taken in late July, but not on 11 other specimens taken in the same period. A female obtained on 20 August was in complete new pelage. The ears of the male shot in Porcupine Draw were infested by chiggers, *Leptotrombidium myotis* (Ewing).

The taxonomic status of Keen's myotis in the Black Hills merits further investigation. I concur with the opinion of Jones and Genoways (1967b:185-186) that individuals from the Hills fall within the currently understood range of variation of *M. k. septentrionalis* from Kansas, Nebraska, Iowa, and eastern South Dakota (Tables 6 and 7). Although there are no significant sexual differences among Black Hill specimens, females are slightly larger than males in all external and cranial measurements. The pelage of females is also slightly paler in tone of color and more intense in reflectance of reds and blues; whereas the pelage of males reflects greens more intensely. The average breadth of the zygomatic arch, braincase, upper molars, and mastoid (excluding specimens from Iowa and Kansas) is narrower in individuals from the Hills than in specimens from areas to the east and southeast. Moreover the forearms of the specimens from the Hills are slightly shorter (excluding those from eastern South Da-

TABLE 6.—Geographic variation in selected external and cranial measurements of adult *Myotis keenii* from the central United States.

Number and sex of specimens averaged	Total length	Forearm length	Zygomatic breadth	Breadth of braincase	Breadth across upper molars	Mastoid breadth
37 (31♂, 6♀)			Black Hills, South Dakota and Wyoming			
Mean	89.0	34.9	8.9	7.1	5.5	7.6
SD	±3.49	±1.06	±0.20	±0.25	±0.15	±0.22
4 (2♂, 2♀)			Bon Homme County, South Dakota			
Mean	87.0	34.7	9.3	7.3	5.7	7.9
SD	±3.37	±0.77	±0.22	±0.08	±0.03	±0.16
12 (5♂, 7♀)			Sarpy County, Nebraska			
Mean	92.5	35.4	9.3	7.5	5.7	7.7
SD	±5.18	±0.76	±0.38	±0.32	±0.18	±0.24
11 (3♂, 8♀)			Boone, Hardin, and Keokuk counties, Iowa			
Mean	88.6	36.1	9.1	7.2	5.6	7.5
SD	±4.63	±0.95	±0.20	±0.16	±0.20	±0.17
12 (7♂, 5♀)			Marshall County, Kansas			
Mean	87.1	35.1	9.1	7.4	5.7	7.5
SD	±3.89	±0.82	±0.22	±0.25	±0.11	±0.18

kota), and their total body length is greater (excluding those from Nebraska). Additional measurements (not listed in Table 6) of 37 specimens from the Black Hills are: tail length, 39.4±2.57; hind foot length, 9.5±0.56; ear length, 17.2±0.90; greatest length of skull, 14.9±0.29; and maxillary toothrow length, 5.8±0.17.

There are no significant geographic differences in the color of pelage of individuals collected in the summer; however, Keen's myotis from the Black Hills are darker on the average than those from Nebraska, Kansas, and eastern South Dakota. Reflectance of hues also varies geographically (Table 7). Specimens from the known population nearest the Hills (Bon Homme County, South Dakota) reflect reds and blues less intensely, and greens more intensely than representatives from the Hills.

Specimens examined (42).—SOUTH DAKOTA: *Pennington County:* Moon, 22 mi W Hill City, 6200 ft, 7; Porcupine Draw, 14 mi W Hill City, 6400 ft, 1; Ice Cave, 8 mi N, 15 mi W Custer, 6400 ft, 9; T. 2 S, R. 6 E, E ½ sec. 19, 1 (MSWB); 10.5 mi E Wyoming border, 5.8 mi N Custer County line, 8 (MSWB). *Custer County:* Elk Mountain, 1 (USNM); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 10 (2 SDMT; 8 UK); Custer State Park, 2 (UMMZ).

WYOMING: *Weston County:* 0.5 mi E Buckhorn, 6100 ft, 3.

Myotis leibii ciliolabrum (Merriam)

SMALL-FOOTED MYOTIS

Vespertilio ciliolabrum Merriam, 1886, Proc. Biol. Soc. Washington, 4:2, 17 December (type locality, a bluff on Hackberry Creek, about one mile from Castle Rock, near Banner, Trego Co., Kansas).

Myotis leibii ciliolabrum—Glass and Baker, 1965, Bull. Zool. Nomenclature, 22:204-205, August.

The small-footed myotis is known from all five counties that comprise the South Dakotan portion of the Black Hills, but it has not been reported previously from northeastern Wyoming. This bat, which has been taken in the Hills year-round, is known to hibernate in Jewel Cave, Davenport Cave, and in an unnamed limestone cave in Dark Canyon, Pennington County. Robert A. Martin (pers. com.) recently has located the

TABLE 7.—Geographic variation in coloration of the mid-dorsal pelage of adult *Myotis keenii* obtained in summer from the central United States.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
19 (14♂, 5♀)		Black Hills, South Dakota and Wyoming		
Mean	16.4	54.2	24.3	21.5
SD	±1.77	±0.22	±0.19	±0.17
4 (2♂, 2♀)		Bon Homme County, South Dakota		
Mean	19.4	53.0	25.7	21.3
SD	±1.65	±0.20	±0.17	±0.13
6 (3♂, 3♀)		Sarpy County, Nebraska		
Mean	17.7	56.3	24.6	19.1
SD	±4.73	±0.40	±0.21	±0.22
9 (3♂, 6♀)		Boone, Hardin, Keokuk counties, Iowa		
Mean	15.2	55.5	25.2	19.3
SD	±1.77	±0.25	±0.13	±0.25
3 (2♂, 1♀)		Marshall County, Kansas		
Mean	16.7	55.8	23.2	21.0
SD	±2.31	±0.46	±0.16	±0.42

species in additional hibernacula such as the Cleopatra Mine, S and G Cave, French Creek Cave, and Igloo Cave. Altitude does not seem to be limiting inasmuch as *Myotis leibii* occurs throughout the Hills up to at least 6500 feet. It was reported first from the region by Miller and Allen (1928:169).

On 2 July 1965, a horizontal shaft in the deserted Cambria Coal Mine complex north of Newcastle, Wyoming, was netted and yielded five *M. leibii* and one *M. thysanodes*. Two more *leibii* were shot over a nearby stock pond on the following evening and another was netted in the mine shaft.

On 19 November 1967, a single male was found hibernating in a cave in Dark Canyon (see account of *L. noctivagans*). The bat was wedged in a horizontal crevice wherein the ambient temperature was 7.2°C. Four solitary males taken from Jewel Cave on 20 November 1967 had rectal temperatures of 6.4°, 7.1°, 7.5°, and 8.0°C; corresponding ambient temperatures were 5.6°, 5.6°, 7.2°, and 6.7°C. Approximately 600 *P. townsendii* were in Jewel Cave at this time. On 7 February 1970, four male *M. leibii* were found hibernating in French Creek Cave located in Custer State Park (see account of *E. fuscus*).

Small-footed myotis taken in the course of this study usually were found near a source of water. Two males and three females were shot in mid-June as they foraged over a stock pond that formed the dammed upper portion of a pine-filled draw near Minnekahta. A male was shot in early July as it flew over Boxelder Creek, near Nemo, and another was shot in late July as it flew over the Savoy Reservoir in Little Spearfish Canyon. Two males were netted over a woodland pond near Moon on 30 July 1968 (see account of *L. borealis*), and another was shot over a reservoir at Roby Springs on 6 September. At several localities, *M. lucifugus, M. keenii, M. thysanodes, M. volans, L. noctivagans, E. fuscus,* and *Lasiurus cinereus* have been shot or netted as they foraged in the same areas as *M. leibii*.

This species retires to night roosts after feeding, as do most other kinds of vespertilionids. All specimens from the

Cambria Coal Mine were entering the shaft when netted between 21:15 and 22:25 hrs (MDT). While collecting in Little Spearfish Canyon in late July and early August 1967, I located a well-used night roost above Timon Campground. One entrance to the cave was about three feet in diameter, but a second entrance, 10 by 15 feet, opened out over the sheer 200-foot cliff. Most of the cave was open, roomy, and well lighted; however, to the rear, an elongate, narrow chimney rose about 40 feet above the ceiling. Although the cave often was visited during the day, only one bat (a male *P. townsendii*) was taken; nevertheless, at night several bats were seen clinging to the walls of the chimney while many others flew in and out of the large entrance overlooking the cliff. One male *M. leibii*, five *M. lucifugus*, and 10 *M. volans* were collected in the roost at this time (Turner and Jones, 1968:444). On 30 July 1968, Wayne H. Davis and I returned to the roost. We spent the night within the cave and established a net angling across the cavern; two additional male *M. leibii* were taken, along with 24 *M. lucifugus* and 42 *M. volans* (Turner and Davis, 1970:361).

Although widespread throughout the Hills, populations of the small-footed myotis seemingly are relatively small. However, on 24 July 1968, Davis, Roger Barbour, and I captured 48 individuals (five females and 43 males) in a net set back within the entrance of Jewel Cave; 35 of these were banded and released (see account of *M. lucifugus*). Thus, small-footed myotis may congregate at favorable sites in the Black Hills.

Females of this saxicolous species usually bear only a single young. Jones and Genoways (1967b:187) reported that no embryos were found in the South Dakotan specimens examined by them and that most individuals collected in the summer were males. Of three females obtained near Minnekahta in mid-June 1967, one contained an embryo that was 8 in crown-rump length. A female taken northeast of Rapid City on 17 July 1945 carried an embryo that was 13. Testicular lengths of 17 males obtained from mid-June to late July were 3 or 4, whereas those of three November-taken males were 2. The two males from Moon and many of the specimens from Jewel Cave were subadults in conspicuous molt.

Small-footed myotis from the Black Hills are parasitized by a chigger, *Leptotrombidium myotis* (Ewing), and a female from Jewel Cave harbored a bat bug, *Cimex pilosellus* (Horvath).

Specimens examined (66).—SOUTH DAKOTA: *Lawrence County:* Cleopatra Mine, 1.5 mi N Carbonate, 2 (SDMT); Little Spearfish Canyon, Savoy, 8 mi W Lead, 5200 ft, 1; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 6000 ft, 3; 2 mi W Nemo, 4700 ft, 1. *Meade County:* Davenport Cave, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 5 (NRW). *Pennington County:* 8 mi ENE Rapid City, 1 (UMMZ); Rapid City, 1 (SDMT); Dark Canyon, 2 mi S, 5 mi W Rapid City, 3800 ft, 1; Diamond S Ranch, near Rapid City, 1 (UMMZ); Moon, 22 mi W Hill City, 6200 ft, 2; Porcupine Draw, 14 mi W Hill City, 6400 ft, 1; Igloo Cave, 3 mi S, 16 mi W Hill City, 2 (SDMT); T. 2 S, R. 6 E, E ½ sec. 19, 1 (MSWB). *Custer County:* 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 1; Hell's Canyon, 13 mi W Custer, 3 (USNM); Custer, 1 (AMNH); French Creek Cave, Custer State Park, 4 (SDMT); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 20 (1 NRW, 1 SDMT, 4 UK, 1 UW); S and G Cave, 11 mi SW Custer, 1 (SDMT). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 5.

WYOMING: *Weston County:* Cambria Coal Mine, 6 mi N Newcastle, 6000 ft, 8.

Additional record.—SOUTH DAKOTA: *Custer County:* Wind Cave National Park (Peck, 1964:38).

Myotis lucifugus carissima Thomas

Little Brown Myotis

Myotis (*Leuconoe*) *carissima* Thomas, 1904, Ann. Mag. Nat. Hist., ser. 7, 13:383, May (type locality, Yellowstone National Park, Wyoming).

Myotis lucifugus carissima—Cary, 1917, N. Amer. Fauna, 42:43, 3 October.

Myotis lucifugus is distributed throughout the northern half of North America and evidently widespread and fairly common in the Black Hills. The known altitudinal distribution of this species extends up to 6900 feet. With

the exception of three individuals obtained in mid-August and one taken in early September, all specimens examined were collected in June and July. Only two females (from Crook County, Wyoming) taken on 1 July 1947 and 24 August, 1913, were among the specimens studied, although Jewel Cave has been reported as a hibernaculum for both sexes (Jones and Genoways, 1967b:187).

In the summer, females ordinarily segregate in nursery colonies; this may account for their scarcity at this time. On 4 July 1970, Robert A. Martin (pers. com.) set a mist net between two chimneys in the attic of the Bob Marshall Camp dining hall, located on the shores of Bismark Lake, about 1 mi E Custer. In the morning, the net yielded seven adult females, one subadult male, and a newly born young. Martin estimated that 100 to 150 adults comprised the nursery colony. To my knowledge, this is the first report of a maternity colony of *M. lucifugus* in the Black Hills region. Martin also captured two females in Rapid City in the summer of 1970.

Myotis lucifugus carissima contrasts with *M. l. lucifugus* of eastern South Dakota in being conspicuously more pale and in having larger average external and cranial dimensions (Jones, 1964:86 and Table 5). The subspecific name *carissima* was assigned to specimens from the Wyoming portion of the study area by Miller and Allen (1928:52), and later to specimens from South Dakota by Jones and Genoways (1967b:187).

Many little brown myotis collected in the course of this study were collected (shot or netted) while the bats were foraging over water, grassy meadows or along the edge of stands of ponderosa pine or white spruce; several individuals were netted at cave entrances as well. Some typical situations in which *M. lucifugus* were obtained are as follow: in early July 1965 seven individuals were collected, along with two *M. volans*, over a beaver pond near Beaver Creek Campground, where the greatest activity occurred just after dark: two were shot on 3 July 1967 over a stock pond in a bluegrass meadow 1 mi E Nemo along with one *Lasiurus cinereus*, one *Lasionycteris noctivigans*, and one *Eptesicus fuscus;* one was netted on the same date over Boxelder Creek, in Lawrence County along with seven *L. cinereus* and one *E. fuscus;* one was shot as it flew over a reservoir at Roby Springs on 6 September 1968; two more were netted over a woodland pond at Moon, one each on 30 July and 20 August 1968 (see account of *L. borealis*); another was netted on 26 July 1968 at the entrance of Ice Cave (see account of *M. thysanodes*).

On 13 June 1965, members of a field party from the Museum of Natural History obtained 12 *M. lucifugus*, five *M. volans* and a mummified *Plecotus townsendii* from Jewel Cave. The majority of the *Myotis* were located in the "dungeon" portion that was wet with seepage water and had an ambient temperature of 6.7°C; all were torpid. Five *M. lucifugus*, 48 *M. leibii*, eight *M. keenii*, 10 *M. volans*, one *E. fuscus*, and four *P. townsendii* were netted at the entrance to Jewel Cave on 24 July 1968; most of the bats were entering the cavern at the time of capture, between dusk and midnight. Five little brown myotis were caught at a night roost in Little Spearfish Canyon in late July of 1967 (see account of *M. leibii*), and another 24 (of which 14 were banded and released) were netted there on 30 July 1968.

The average testicular length of 25 males taken in June and July was 4.2 (2-7). A female, with a young attached, was extracted from a crack in the wall of a summer cottage 15 mi ENE Sundance, Wyoming, on 1 July 1947.

Molt was apparent in an adult male taken on 7 July 1965, in Pennington County, because new pelage was observed underlying the old in the middorsal region and behind the ears. Several individuals from Little Spearfish Canyon, obtained on 30 July, were subadults in conspicuous molt. An albinistic little brown bat was captured in Jewel Cave on 31 August 1966 by L. N. Brown

and associates of the University of Wyoming.

A male taken at Moon on 20 August 1968 was parasitized externally by bat flies, *Basilia forcipata* Ferris, and by laelaptid mites, *Macronyssus crosbyi* (Ewing and Storer). *Myotis lucifugus carissima* from many localities in the Hills harbored chiggers, *Leptotrombidium myotis* (Ewing). In a report filed at Wind Cave National Park, Olaf E. Ryberg recorded another species of bat fly, *Trichobius corynorhinus* Cockerell, on specimens taken at Jewel Cave in May 1962.

Specimens examined (84).—SOUTH DAKOTA: *Lawrence County:* Little Spearfish Canyon, Savoy, 8 mi W Lead, 5200 ft, 3; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 6000 ft, 15; 2 mi W Nemo, 4700 ft, 4; 3 mi E Nemo, 4700 ft, 1; 1 mi E Nemo, 4700 ft, 3. *Meade County:* Haven Dams, 6 mi S, 1.5 mi W Sturgis, 4600 ft, 1. *Pennington County:* Rapid City, 1 (NRW); Sitting Bull Cave, 1 (SDMT); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 8; 3 mi N, 7 mi W Deerfield, 6900 ft, 1; Moon, 22 mi W Hill City, 6200 ft, 2 (1 UK); Ditch Creek, 14 mi W Hill City, 6400 ft, 2; T. 2 S, R. 6 E, E ½ sec. 19, 1 (MSWB); 10.5 mi E Wyoming border, 5.8 mi N Pennington-Custer county line, 6 (MSWB). *Custer County:* 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 1; Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 27 (2 SDMT, 8 UW, 5 UK); Housing Area, Wind Cave National Park, 4100 ft, 2 (WCNP). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 1.

WYOMING: *Crook County:* Sand Creek, 3750 ft, 2 (USNM); 15 mi ENE Sundance, 3825 ft, 1.

Additional records (see text also).—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB).

Myotis thysanodes pahasapensis Jones and Genoways

FRINGE-TAILED MYOTIS

Myotis thysanodes pahasapensis Jones and Genoways, 1967, Jour. Mamm., 48:231-235, 20 May (type locality, 6 mi N Newcastle, 6000 ft, Weston Co., Wyoming).

On 2 July 1965, I removed a fringe-tailed myotis from a net stretched across a horizontal shaft in the deserted Cambria Coal Mine complex, 6 mi N Newcastle, Weston Co., Wyoming. This male subsequently was designated as the holotype of *Myotis thysanodes pahasapensis*, a subspecies restricted to the Black Hills and adjacent areas. The range of this subspecies is disjunct from the more western range of *M. t. thysanodes* by approximately 400 miles (Jones and Genoways, 1967a:234; 1967b:188). In South Dakota, *Myotis thysanodes* has been taken only from Pennington, Custer, and Fall River counties, and in Wyoming only from Weston County. Its known altitudinal range in the Hills is between approximately 3800 and 6200 feet.

Thirty years intervened between the first report (Bole, 1935:147-148) and the second report (Thompson, 1965:37) of this species in the Hills region. In the interim, a young female from Custer State Park (Stebler, 1939:389) and an adult male from 1.5 mi E Buckhorn, Wyoming (Long, 1965:532) were reported as *Myotis evotis*.

The fringe-tailed myotis resides in the Black Hills the year around, as evidenced by a hibernating male taken in a cave along Boxelder Creek near Dody Spring, in Pennington County, on 17 February 1968 (Turner and Jones, 1968: 445). Methods of capture of specimens collected previously are unknown. Individuals obtained in the present study either were shot or netted as they foraged in the following areas: 1) over water—one female (5 July 1966) over a stream 3 mi N Hot Springs; one female (13 July 1967) over a stock pond in a pine-filled draw near Minnekahta; one male (30 July 1968) and two females (30 July and 20 August 1968, respectively) over a woodland pond near Moon (see account of *L. borealis;* 2) over a grassy meadow—a male (19 July 1951) feeding at dusk 1.5 mi E Buckhorn in company with one *Eptesicus fuscus;* 3) at the entrances of caves—one female and five males (July and August, 1965-66) and one male (17 February 1970) at Jewel Cave (see account of *M. lucifugus*); two males (26 July 1968) at Ice Cave (see account of *E. fuscus*); 4) at the opening of a mine shaft—the holotype of *pahasapensis* (taken along with *M. leibii*). In addition, three females

were taken in mid-June 1968 while in a day roost, which was situated among the rafters of an open porch in Wind Cave National Park; these fringe-tailed myotis were clustered in close association with *M. volans* (Turner and Davis, 1970: 361).

When Wayne H. Davis and I netted the entrances to Ice Cave on 26 July 1968, a flurry of activity occurred between 21 and 22 hrs (MDT), and gradually decreased thereafter. Nine *M. keenii*, one *M. lucifugus*, 20 *M. volans*, and four *E. fuscus* were captured with *M. thysanodes*. The large mass of natural ice that persists in the cavern, even in summer, is indicative of the cool temperatures therein.

Each of the three females obtained at Wind Cave National Park on 15 June carried a single embryo; they were 6, 8, and 12 in crown-rump length. Lactating females were taken at Moon on 30 July and 20 August. A male also captured on 30 July had testes that were 5 in length. Young of the year were noted flying as early as 10 August.

New hairs were found beneath the old pelage of males taken in late July. Molt had not begun on a female taken at the same time, but it was relatively far advanced on a female obtained on 20 August. Three pregnant females captured at Wind Cave National Park on 15 June were molting over both dorsum and venter.

A female fringe-tailed myotis from Fall River County harbored a bat fly, *Basilia forcipata* Ferris, chiggers, *Leptotrombidium myotis* (Ewing), and a bat bug, *Cimex adjunctus* Barber. Dr. George W. Byers, Department of Entomology, The University of Kansas, identified the remains of a moth, a small scarabid beetle, and a large alleculid beetle from the stomach of this same individual.

In contrast with *Myotis evotis*, which the fringe-tailed bat resembles superficially, *Myotis thysanodes* possesses a longer forearm, shorter ears, slightly larger cranial dimensions, a conspicuous fringe of hairs on the free border of the uropatagium, a better developed sagittal crest, a slightly higher and more inflated braincase, and somewhat more robust teeth (see Jones and Genoways, 1967a: 233-234; 1967b:189). Although *M. evotis* occurs over much of Wyoming and western South Dakota, no specimens have been obtained in the Black Hills. Jones and Genoways (*loc. cit.*) suggested that *thysanodes* and *evotis* might be ecologically separated.

Fringe-tailed myotis from the Black Hills differ from *M. t. thysanodes* in having larger ears, shorter forearms, more contrast in color between dorsal pelage and membranes, and a smaller skull that is relatively narrow (Jones and Genoways, 1967a:233). After preliminary analysis for secondary sexual variation, the pelage of individuals collected in the summer from east-central California (Tuolumne County) and from Cocomino, Cochise, and Gila counties, Arizona, was compared with that of representatives from the Black Hills. Californian specimens are significantly darker in color tone than those from either Arizona or the Black Hills. Major differences between the latter two populations are the greater reflection of greens by representatives from the Hills and the slightly lighter tone of the individuals from Arizona. Average measurements and standard deviations of pelage color of 10 (four males and six females) adult *M. t. pahasapensis* collected in the summer are: color tone, 25.3±4.22; percent red reflectance, 55.0±0.56; percent green reflectance, 20.1±0.29; and percent blue reflectance, 24.9±0.36. Selected average measurements and standard deviations of 16 specimens, nine males and seven females, of fringe-tailed myotis from the Black Hills are: total length, 94.4±3.22; tail length, 41.0±1.94; hind foot length, 10.6±0.92; ear length, 18.5±0.95; forearm length, 41.1±1.20; greatest length of skull, 16.6±0.27; zygomatic breadth, 10.1±0.21; interorbital constriction, 3.9 ±0.14; braincase breadth, 7.7±0.19; mastoid breadth, 8.3±0.19; breadth across upper molars, 6.5±0.22; maxillary tooth-row length, 6.3±0.16; and breadth across upper canines, 3.9±0.18.

Specimens examined (30).—SOUTH DAKOTA: *Pennington County:* along Boxelder Creek, near Dody Spring, 4060 ft, 1; Moon, 22 mi W Hill City, 6200 ft, 3; Ice Cave, 8 mi N, 15 mi W Custer, 6400 ft, 2 (UK); 10.5 mi E Wyoming border, 5.8 mi N Pennington-Custer county line, 7 (MSWB). *Custer County:* Grace Coolidge Creek, Custer State Park, 1 (UMMZ); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 9 (3 SDMT, 1 UMMZ, 4 UW); Elevator Building, Wind Cave National Park, 4100 ft, 3; 3 mi N Hot Springs, 1 (UW). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 1.

WYOMING: *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 1; Cambria Coal Mine, 6 mi N Newcastle, 6000 ft, 1.

Myotis volans interior Miller

LONG-LEGGED MYOTIS

Myotis longicrus interior Miller, 1914, Proc. Biol. Soc. Washington, 27:211, 31 October (type locality, 5 mi S Twining, 11,300 ft, Taos Co., New Mexico).

Myotis volans interior—Miller and G. M. Allen, 1928, Bull. U. S. Nat. Mus., 144:142, 25 May.

Myotis volans, first reported in the study area by Moulthrop (1936:413), is known throughout the Black Hills, except from Crook County, Wyoming. Evidently this is the most common and widely distributed species of the genus in the region. In general, this species occupies montane areas of western North America. The known altitudinal range in the Black Hills is 4000 to 6500 feet, but the species is most abundant above 4500 feet. It is resident throughout the year as evidenced by hibernating individuals taken from Bush's Cave (20 November) and Jewel Cave (20 to 26 November and 17 February).

The long-legged myotis superficially resembles the little brown myotis, but *M. volans* differs from *M. lucifugus* in having a shorter rostrum, a braincase that is abruptly elevated from the rostral level, low rounded ears, a keeled calcar, and pelage that usually extends onto the underside of the wing to a line joining the elbow and knee.

Myotis volans forages over such areas as campgrounds, meadows, and water courses. For example, in early June 1965, 11 individuals were shot at dusk as they flew through Ditch Creek Valley and associated Porcupine Draw in Pennington County (see account of *M. keenii*). Five males and two females were taken in company with one *M. leibii* over a reservoir at Roby Springs, Custer County, in early September 1968. Five males and two females (four of these bats were banded and released) were netted over ponds near Moon in late July and mid-August of 1968 (see account of *L. borealis*). A female, evidently disturbed from her daytime roost, was captured in mid-morning (10:30 A.M., MDT) at the Beaver Creek Campground, Pennington County, on 13 June 1965. A male collected at this same site on 2 July 1965 carried the remains of a crane fly (Tipulidae) in his mouth.

Caves are utilized in summer by *M. volans* both as daytime retreats and as nighttime roosts following foraging flights. Individuals have been obtained during the summer from Bear Trap Cave, Ice Cave (19 banded and released on 24 July 1968), and Jewel Cave. (Five torpid bats were obtained in the latter cavern on 13 June 1965; see account of *M. lucifugus.* Nine *M. volans* were banded and released in Jewel Cave on 24 July 1968.) On 5 July 1967, I shot a male about 10:30 P.M. (MDT) as it flew into Davenport Cave and alighted on a crystalline calcite (dog-tooth spar) wall. Ten males were collected from a night roost in Little Spearfish Canyon between 26 July and 7 August 1967 (see account of *M. leibii*), and 42 males were netted, banded, and released in this same cavern on 30 July 1968. All chiropteran species known to occur in the Black Hills were associated with *M. volans* at some locality. On two different occasions, individuals were located in a day roost on Wind Cave National Park in company with *M. thysanodes.* Eleven of these were banded and released, and a female was netted one month later within 200 yards of the original site of capture (Turner and Davis, 1970:362).

On 20 November 1967, a single male was taken in Bush's Cave, a small cave several hundred feet south of the en-

trance to Jewel Cave. The ambient temperature was 9.7°C and the rectal temperature of the bat, which was torpid and covered by droplets of moisture, was 10.6°C. A single *Plecotus townsendii* also was noted in Bush's Cave at that time.

Jones and Genoways (1967b:190) reported two females, each containing a single embryo, that were obtained on 29 and 30 June in Harding County, north of the Hills. However, of 18 females collected in the summer and examined from the Hills region, none was lactating and only one was pregnant. The latter specimen was taken in Wind Cave National Park on 25 July and the single embryo was 16 in crown-rump length. A male flying young of the year was obtained at Roby Springs on 7 September. Testes of 14 males taken from mid-June to late July were 1 to 5 in length.

New hairs were manifest under the old pelage over much of the body of a male taken on 30 July 1961. Bat flies, *Basilia forcipata* Ferris, were found on *M. volans* from Pennington, Custer and Fall River counties, whereas other individuals from Pennington, Fall River, and Lawrence counties harbored chiggers, *Leptotrombidium myotis* (Ewing). Two females from Wind Cave National Park were infested by spinturnicid mites, *Spinturnix americanus* (Banks), and a male from Roby Springs, Custer County, was parasitized externally by several unidentifiable (badly damaged) mites.

Specimens examined (77).—SOUTH DAKOTA: *Lawrence County:* 2 mi S Tinton, 6100 ft, 1; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 6000 ft, 10; 2 mi W Nemo, 4700 ft, 1. *Meade County:* Davenport Cave, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 1. *Pennington County:* Rapid City, 3 (NRW); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 3; Moon, 22 mi W Hill City, 6200 ft, 3; Ditch Creek, 14 mi W Hill City, 6400 ft, 11; Ice Cave, 8 mi N, 15 mi W Custer, 6400 ft, 1; Bear Trap Cave, 4 mi S, 16 mi W Hill City, 6000 ft, 1; T. 2 S, R. 6 E, E ½ sec. 19, 1 (MSWB); 10.5 mi E Wyoming border, 5.8 mi N Custer County line, 8 (MSWB); unspecified locality, 1 (NRW). *Custer County:* Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 7; Bull Springs, 2 mi N, 9 mi W Custer, 6500 ft, 1 (UMMZ); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 12 (3 NRW, 1 SDMT, 1 UW); Headquarters, Wind Cave National Park, 4100 ft, 1 (UMMZ); Elevator Building, Wind Cave National Park, 4100 ft, 1; Housing Area, Wind Cave National Park, 4100 ft, 5. *Fall River County:* 5.5 mi E Minnekahta, 4000 ft, 1; 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 2.

WYOMING: *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 1; Cambria Coal Mine, 6 mi N Newcastle, 6000 ft, 1.

Additional record.—SOUTH DAKOTA: *Custer County:* Wind Cave, Wind Cave National Park (Peck, 1964:39).

Lasionycteris noctivagans (Le Conte)

Silver-haired Bat

V[*espertilio*]. *noctivagans* Le Conte, 1831, in McMurtrie, The animal kingdom . . . by the Baron Cuvier . . ., 1:431 (type locality, eastern United States).

[*Lasionycteris*] *noctivagans*—Peters, 1866, Monatsb. k. preuss. Acad. Wiss., Berlin, p. 648 (for 1865).

The silver-haired bat occurs throughout the United States, but is known in the Black Hills from only seven localities in South Dakota; all but two specimens were obtained in transitional areas between the high plains and foothills along the southern and eastern periphery of the Hills. This species first was reported in the study area by Jones and Genoways (1967b:190). Although little is known of the actual migratory routes, *Lasionycteris* presumably migrates through the Hills region (northward in spring and southward in late summer and early autumn). Jones and Genoways (*loc. cit.*) suggested that this species probably is resident in the higher part of the Black Hills in summer. The altitudes at which most individuals have been collected thus far generally range from 3800 to 4700 feet, but two males were obtained at 6200 feet near Moon on 29 July, 1968 (see account of *L. borealis*). Thus, the silver-haired bat is more widely distributed altitudinally than previously supposed.

There are few records of silver-haired bats occurring in caves. A solitary male was taken from an unnamed cave in Dark Canyon on 19 November 1967 in a semitorpid state. The limestone cave is lo-

cated about 90 feet below the crest of a 200-foot cliff. Relative humidity within the cave was 57 percent, and the ambient temperature was 6.7°C; rectal temperature of the bat was 9.6°C. The male was hidden in a horizontal crevice and became somewhat active shortly after being extracted. Three *Plecotus townsendii* and one *Myotis leibii*, all in a torpid state, also were collected in the same cavern at this time. The lateness of the season, the low rectal temperature, and the situation in which the bat was found, all suggest that this individual was not a late transient, but rather in hibernation (Turner and Jones, 1968:445). Thus, it is probable that at least a few silver-haired bats reside in the Black Hills throughout the entire year.

In 1967, five individuals, two from southwest of Minnekahta (12 and 13 June) and three from near Nemo (29 June to 3 July), were shot as they foraged in early evening in company with *Myotis leibii, M. lucifugus, M. thysanodes, Eptesicus fuscus,* and *Lasiurus cinereus.* Another individual was captured at the former site at 13:30 (MDT) on 14 June in a net over a small algae-covered pond, and a male was captured in a net set over a sewage settling pond at the head of Wind Cave Canyon on 25 July 1968. This species seems to prefer to forage in grassy valleys that contain a source of standing water and which are surrounded by hillsides well-forested with ponderosa pine.

Females give birth to one or usually two young between late May and early July. A female shot near Minnekahta on 12 June 1967 carried two embryos that were 11 in crown-rump length. Length of the testes of five males taken from 13 June to 3 July 1967 varied between 4 and 5; a male obtained in November had a testicular length of 4. The testes of three males obtained in late July 1968 were 6, 7, and 7 in length. Fine silver-tipped hairs were seen underlying the old pelage on the dorsum of the three latter individuals.

A male from Minnekahta, Fall River County, was parasitized externally by chiggers, *Leptotrombidium myotis* (Ewing), whereas the male from Dark Canyon harbored laelaptid mites, *Macronyssus unidens* Radovsky. In addition, B. V. Peterson, Entomology Research Institute, Ottawa, Ontario, identified a bat fly found on a male *L. noctivagans* from Wind Cave National Park as either *Trichobius adamsi* Auguston or a new species; *T. adamsi* has been reported previously only from *Macrotus californicus* and *Tadarida brasiliensis.*

Specimens examined (11).—SOUTH DAKOTA: *Lawrence County:* 2 mi W Nemo, 4700 ft, 2; 1 mi E Nemo, 4700 ft, 1. *Pennington County:* Diamond S Ranch, near Rapid City, 1 (UMMZ); Dark Canyon, 2 mi S, 5 mi W Rapid City, 3800 ft, 1; Moon, 22 mi W Hill City, 6200 ft, 2. *Custer County:* Wind Cave Canyon, Wind Cave National Park, 4100 ft, 1. *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 3.

Eptesicus fuscus pallidus Young

BIG BROWN BAT

Eptesicus pallidus Young, 1908, Proc. Acad. Nat. Sci. Philadelphia, 60:408, 14 October (type locality, Boulder, Boulder Co., Colorado).

Eptesicus fuscus pallidus—Miller, 1912, Bull. U. S. Nat. Mus., 79:62, 31 December.

The pallid big brown bat, originally reported from the region as *Adelonycteris fusca* (J. A. Allen, 1895a:273), is common, widespread, and occurs in all counties that comprise the Black Hills. This species inhabits most of North America and is known in the study area from elevations between 3500 and 6200 feet. *Eptesicus fuscus pallidus* differs from *E. f. fuscus* which is geographically adjacent to the east in South Dakota in its discernibly paler pelage, and smaller average external and cranial dimensions (Jones, 1964:92).

Most of the specimens examined were collected in summer; however, individuals have been obtained in the winter at Custer (23 January 1888) by Vernon Bailey, in Hell's Canyon (5 January 1902) by Merritt Cary, and in hibernacula such as Jewel Cave (Jones and Genoways, 1967b:192). On 7 February 1970,

Robert A. Martin and associates (pers. com.) located a winter colony of 20 *E. fuscus*, four *Myotis leibii*, and two *Plecotus townsendii* in a cave along French Creek in Custer State Park; all bats found in the cavern at that time were males.

While attempting to obtain flying squirrels in a spruce-filled canyon on 11 February 1946, J. A. King captured a female big brown bat by the wing in a rat trap; the trap was attached about seven feet above the ground to a tree, and peanuts were used as bait. The local conditions under which this unseasonal activity occurred are unknown to me. King later collected a male (4 March 1946) and a female (21 March 1946) that were hibernating in an old horizontal mine shaft in the same area (3 mi SE Hill City, Pennington County).

Many of the big brown bats collected in this study were shot at dusk as they foraged over grassy, conifer-bordered meadows, or over ponds and water courses (Turner and Jones, 1968:446). Others were captured in mist nets in the following situations: One male (3 July 1967) captured as it flew along Boxelder Creek, 2 mi W Nemo (see account of *M. lucifugus*). Four males (29 July 1968; three banded and released) netted while foraging over a woodland pond near Moon (see account of *L. borealis*). One male (24 July 1968) taken at the entrance to Jewel Cave (see account of *Myotis lucifugus*). Four males and one female (26 July 1968; four banded and released) netted at the entrance of Ice Cave. The main activity of 32 bats taken in the last-mentioned cavern was between 21 and 22 hrs (MDT); however, big brown bats were not obtained until about 23 hrs (see account of *Myotis thysanodes*). Other species taken along with *Eptesicus* at various sites of capture were *Myotis keenii*, *M. leibii*, *M. lucifugus*, *M. thysanodes*, *M. volans*, *Lasionycteris noctivagans* and *Lasiurus cinereus*.

On 27 July 1967, I captured a female that carried two embryos (8 in crown-rump length) in the attic of a classroom building on the campus of the Black Hills State College at Spearfish. Females ordinarily give birth to one or two young between May and mid-June in western South Dakota (e.g., a female taken in Fall River County on 14 June carried two embryos that each measured 7 in crown-rump length); thus a pregnant big brown bat in late July would seem exceptional. Returning to the same attic on 29 July I obtained 21 additional *E. fuscus*, of which eight were lactating adult females, five were subadult females, seven were subadult males, and one was an adult male.

Martin (pers. com.) reported that a maternity colony of this species was located on 19 May 1970 in the attic of the Dakota Steel Company in Rapid City. Two other maternity colonies were found in Hot Springs in the summer of 1968. Ten pregnant females (six were banded and released, and four were examined; each of the latter carried a single embryo of an average crown-rump length of 18.5 (15.0-23.0)) and four lactating females were netted in the attic of the Fall River Museum on 25 June and 27 July, respectively. One subadult male and four subadult females were captured in the Fall River County Courthouse on 26 July.

A captive female from the Fall River Museum aborted two young on the night of 25 June (Turner and Davis, 1970: 363). The entire process lasted less than 10 minutes. The female propped herself on the tips of her forearms, lowered her head ventrally toward the vaginal orifice, and actively aided the birth by licking the vaginal region and the emerging young. The young were cradled in the uropatagium, which was curved forward beneath the body of the female. Though seemingly close to exhaustion, the female readily devoured several moths offered to her immediately following the events just described.

Length of testes of 18 adult males obtained between 13 June and 4 July were 5.8 (4.0-7.5). Testicular length of two

adults taken on 29 July 1967 were 9 and 10, whereas that of five subadults captured on the same day were 4.4 (3.0-7.0). A male (banded and released), with large, descended testes, was extracted from a space between a stone chimney and eaves of an overhanging roof of a house in Rapid City on 3 August 1969.

Jones and Genoways (1967b:191) described molt in *E. f. fuscus* and their description seems applicable also to *E. f. pallidus*. Subadults from Spearfish and Hot Springs were undergoing post-juvenal molt late in July, whereas an adult female from Spearfish was in process of annual molt.

Big brown bats from southwest of Minnekahta harbored bat bugs, *Cimex adjunctus* Barber, and ticks, *Ornithodoros kelleyi* Cooley and Kohls, whereas a female from Hot Springs was infested with spinturnicid mites, *Spinturnix bakeri* Rudnick, and a male from Moon sheltered bat flies, *Basila forcipata* Ferris. *Eptesicus* from various localities in the Black Hills were parasitized externally by chiggers, *Leptotrombidium myotis* (Ewing).

Specimens examined (129).—SOUTH DAKOTA: *Lawrence County:* Spearfish, 3600 ft, 22; Little Spearfish Canyon, Savoy, 8 mi W Lead, 5200 ft, 2; 2 mi W Nemo, 4700 ft, 6; 1 mi E Nemo, 4700 ft, 1. *Pennington County:* Rapid City, 5 (4 NRW, 1 SDMT); Diamond S Ranch, near Rapid City, 6 (UMMZ); South Canyon, 3 mi W Rapid City, 12 (AMNH); Moon, 22 mi W Hill City, 6200 ft, 1; Ice Cave, 8 mi N, 15 mi W Custer, 6400 ft, 1; Hill City, 1 (NRW); 3 mi SE Hill City, 5300-5400 ft, 3 (UMMZ); 10.5 mi E Wyoming border, 5.8 mi N Custer County line, 2 (MSWB). *Custer County:* 5.75 mi N, 5.75 mi E Custer, 5220 ft, 5; Hell's Canyon, 13 mi W Custer, 2 (USNM); Custer, 4 (USNM); Squaw [Grace Coolidge] Creek, 1 (AMNH); French Creek Cave, Custer State Park, 8 (SDMT); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 2 (1 UW, 1 WCNP); Headquarters, Wind Cave National Park, 4100 ft, 17 (2 WCNP, 15 UMMZ); Shirttail Canyon, Wind Cave National Park, 2 (UMMZ); Onyx Cave, 10 mi NW Hot Springs, 1 (UW). *Fall River County:* Fall River Museum, Hot Springs, 3600 ft, 8; Courthouse, Hot Springs, 3500 ft, 5; 5.5 mi E Minnekahta, 4000 ft, 1; 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 8.

WYOMING: *Crook County:* Sand Creek, 1 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 1; Cambria Coal Mine, 6 mi N Newcastle, 6000 ft, 1.

Additional record.—SOUTH DAKOTA: *Meade County:* Fort Meade (Miller, 1897:98).

Lasiurus borealis borealis (Müller)

Red Bat

Vespertilio borealis Müller, 1776, Des Ritters Carl von Linné . . . vollstandiges Natursystem . . ., suppl., p. 20 (type locality, New York).

Lasiurus borealis—Miller, 1897, N. Amer. Fauna, 13:105, 16 October.

Turner and Davis (1970:363) recently reported the first specimens of the red bat to be taken west of the Missouri River in South Dakota. Jones and Genoways (1967b:193) suggested that this species probably reached the western limits of its resident range in South Dakota at approximately the 101st meridian, but that migrating individuals might pass through the western part of the state on their way to or from regions farther to the north. Long (1965:534) mentioned an individual (USNM 5264) that was listed by H. Allen (1864:20, 1894:153) from Laramie Peak, as the only specimen known from Wyoming.

Nets were established over two ponds near Moon Campground in Pennington County on 29 July 1968. One net was located in a small meadow in a woodland and the other over a farm pond situated in a pasture. No red bats were taken over the woodland pond, but Wayne H. Davis captured a female young of the year over the farm pond; the latter individual was just beginning post-juvenal molt. Two *Myotis leibii*, two *M. keenii*, two *M. volans*, two *Lasiurus cinereus*, and two *Lasionycteris noctivagans* were removed from this same net, whereas four *M. keenii*, one *M. lucifugus*, two *M. thysanodes*, three *M. volans*, four *E. fuscus* and 13 *L. cinereus* were removed from the net over the woodland pond. Returning to the woodland pond on 20 August, I obtained a lactating female red bat, along with one *M. keenii*, one *M. lucifugus*, one *M. thysanodes*, two *M. volans* and one *L. cinereus*. On the first

visit, the woodland pond was fairly open and activity began about 21 hrs (MDT); a total of 27 bats was netted. In contrast, the pond was well overgrown with vegetation on the second visit. Although the net was observed from 20 until 00:30 hrs, not a single bat was detected; however, when examined early the next morning, the seven bats in the net were concentrated over a small pool of open water. Utilization of the pond by bats evidently decreased greatly as the surface vegetation increased.

The interim (22 days) between capture of the flying young of the year and the lactating female almost certainly excludes the possibility that the young was that of the female. Thus, at least two families of *L. borealis* evidently occurred in the vicinity of Moon during the summer of 1968. Members of this species migrate southward in winter, returning northward again in spring, and additional data are needed to ascertain the summer status of the red bat in the Black Hills.

Specimens examined (2).—SOUTH DAKOTA: *Pennington County:* Moon, 22 mi W Hill City, 6200 ft, 2.

Lasiurus cinereus cinereus
(Palisot de Beauvois)

Hoary Bat

Vespertilio cinereus (misspelled *lincreus*) Palisot de Beauvois, 1796, Catalogue raisonné du muséum de Mr. C. W. Peale, Philadelphia, p. 18 (p. 5 of English edition by Peale and Palisot de Beauvois) (type locality, Philadelphia, Philadelphia Co., Pennsylvania).

Lasiurus cinereus—H. Allen, 1864, Smiths. Misc. Coll., 7 (165):21, June.

The hoary bat has not been reported from the Wyoming section of the Black Hills, but it is known from Lawrence, Pennington, Custer, and Fall River counties of South Dakota. This is the largest of the Black Hills bats and seems to be locally abundant in suitable habitats. Like the red bat, *Lasiurus cinereus* is a migrant, arriving in the Hills region in late spring and residing there until early autumn; seasonal records are from 13 June to 31 August.

Findley and Jones (1964:469) indicated that females generally precede males in the northward migration and occupy the plains and adjacent lowlands in warmer months, whereas the males usually are found at higher altitudes or, occasionally, at higher latitudes. The 28 specimens (11 males and 17 females) taken in this study certainly establish the Black Hills as one of the few areas in the mid-continent region where adult *L. cinereus* of both sexes occur together in summer. In western South Dakota, males occur only in the Black Hills, at elevations of 4700 to 6200 feet, whereas females occupy suitable habitat up to 6400 feet in the Hills and also range down through transitional lower elevations out onto the adjacent plains and lowlands. The first representatives of this species from the Black Hills were reported by Jones and Genoways (1967b:193).

Of 14 hoary bats collected in the vicinity of Nemo between 28 June and 3 July 1967, seven were netted over Boxelder Creek (see account of *M. lucifugus*), and seven others were shot in areas where *M. leibii*, *M. lucifugus*, *M. volans*, *E. fuscus*, and *Lasionycteris noctivagans* also foraged (i.e., over streams and meadows bordered by ponderosa pine). A single male was shot on 19 June 1967 as it foraged over a small valley northeast of Custer, and two females were obtained (one netted over a stock pond, in association with the above mentioned species and *M. thysanodes*, and the other shot as it flew along the edge of a conifer-bordered meadow) southwest of Minnekahta on 13 June 1967. Of 15 hoary bats (11 banded and released) netted over a woodland pond (13 individuals) and a farm pond (two individuals) near Moon on 30 July 1968, six were adult males, six were lactating females, and three were juveniles (one male and two females); an additional male young of the year was obtained over the woodland pond on 20 August 1968 (see account of *L. borealis*). Two female *L.*

cinereus (one lactating and the other a young of the year) were netted over a sewage settling pond at the head of Wind Cave Canyon on 25 July 1968 in company with a *L. noctivagans*.

One or (usually) two young are born from late May to early July. Of two adult females taken on 13 June, one carried two embryos (each being 22 in crown-rump length) and the other was lactating. None of six females taken between 28 June and 3 July was pregnant, but four were lactating; all six adult females obtained at Moon on 29 July, and one collected in Ditch Creek Valley on 13 June, also were lactating. Testes of eight males captured from mid-June to mid-July were 5.4 (4-7) in length.

The subadults collected late in July to mid-August were in fresh pelage. No ectoparasites were found on individuals of this species.

Specimens examined (28).—SOUTH DAKOTA: *Lawrence County:* 2 mi E Tinton, 5400 ft, 1; 2 mi W Nemo, 4700 ft, 13; 1 mi E Nemo, 4700 ft, 1. *Pennington County:* Rapid City, 1 (NRW); Moon, 22 mi W Hill City, 6200 ft, 5 (2 UK); Ditch Creek, 14 mi W Hill City, 6400 ft, 1; 10.5 mi E Wyoming border, 5.8 mi N Pennington-Custer county line, 1 (MSWB). *Custer County:* 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 2. *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 2.

Plecotus townsendii pallescens (Miller)

Townsend's Big-eared Bat

Corynorhinus macrotis pallescens Miller, 1897, N. Amer. Fauna, 13:52, 16 October (type locality, Keam Canyon, Navajo County, Arizona).

Plecotus townsendii pallescens—Handley, 1959, Proc. U. S. Nat. Mus., 110:190, 3 September.

This cavernicolous species is distributed through much of western North America, and is known from all counties that comprise the Black Hills; it was first reported from the study area by G. M. Allen (1916:334) under the name *Corynorhinus megalotis pallescens*. John Tyers and associates of the U. S. National Park Service have banded many individuals in Jewel Cave, where an estimated 2000 big-eared bats hibernate in winter along with *Myotis leibii, M. lucifugus, M. volans,* and *Eptesicus fuscus*. Bats evidently vacate these limestone hibernacula in late spring and disperse throughout the Hills; females congregate in maternity colonies in warm standstone caves or attics of buildings, whereas males seem to remain solitary. Known altitudinal range in the Hills is from 3400 to 6200 feet.

Although large associations of big-eared bats occur in the Hills region, none of the specimens taken in this study was obtained by the usual collecting methods, that is, by netting or shooting. Perhaps the activity patterns of this bat differ from those of other species that occur in the region, and it may remain in retreats until well after dark. V. Bailey, however, reported *P. townsendii* to be among the earliest observed bats flying each evening in the vicinity of Sundance, Wyoming (Handley, 1959:175).

On 4 August 1969, a solitary big-eared bat was observed in a narrow chimney of a small cave on the rim of Little Spearfish Canyon, above Timon Campground; a single male (testes 6 in length) was captured in the cave on 7 August 1970. Although the cavern is used extensively as a night roost (see account of *M. leibii*), *P. t. pallescens* were the only bats that utilized the chimney as a day roost.

On 20 July 1967, I located a nursery colony in a small cave formed in a sandstone bluff at a locality 1 mi S and 2 mi E Hot Springs, Fall River County (Turner and Jones, 1968:447). Of the 41 bats present in the cavern, 22 were adult females; 19 of these were lactating and one carried an embryo that was 27 in crown-rump length. Eight juvenile females and 11 juvenile males (with testicular lengths of 3) comprised the remainder of the colony. The young represented various stages of development and molt (from fine post-natal hair on nearly naked animals to juvenal pelage on well developed young) indicating that dates of parturition within the col-

ony probably extend over a considerable period of time. A solitary male (testes 6 in length) was found in this same cave on 30 June 1968.

A secluded male (testicular length 4) was found clinging to the crystalline calcite (dog-tooth spar) walls of Davenport Cave on 20 November 1967, and three big-eared bats (two males and one female) were found hibernating in an unnamed limestone cave in Dark Canyon on 10 November 1967 (see account of *L. noctivagans*). Although the males were captured deep in the cave, the solitary female was taken in the twilight zone. Testicular length of both males was 3. Ambient temperatures at the sites of capture were 6.4°, 5.3°, and 7.2°C, whereas the rectal temperatures of the bats were 7.2°, 8.0°, and 8.6°C, respectively. Mummified remains of *P. townsendii* were found in Jewel Cave on 13 June 1965, and in the deserted Cambria Coal Mine complex north of Newcastle, Weston County, Wyoming, on 2 July 1965.

Jewel Cave was visited by a field party from the Museum of Natural History on 20 November 1967. Approximately 600 *Plecotus* were wintering there at the time, and 304 of these were examined. Two hundred big-eared bats (69 females and 131 males) were distributed in clusters containing from two to 33 bats; the remaining 104 individuals (40 females and 64 males) were solitary. Ambient temperature ranged from 5.0° to 6.4°C and the relative humidity ranged from 64 to 70 percent in areas occupied by *Plecotus*. The average rectal temperatures of 18 females and 34 males were 4.3°C (3.6-6.2) and 4.2°C (3.6-6.2), respectively; individuals from larger clusters tended to have a mean body temperature 1-2° lower than did solitary individuals or those from small clusters. Most of the bats were within 150 feet of the entrance, where the ambient temperature was lower than deeper in the cave. Air currents made this general area susceptible to environmental fluctuations.

A plug that completely filled the vaginal orifice was observed in many of these females when rectal temperatures were taken. Thomas H. Kunz examined seven vaginal smears under a phase contrast microscope and found numerous agglutinated clumps of sperm in the semen suspension. Pearson *et al.* (1952: 293) indicated that vaginal plugs were not found in *Plecotus townsendii* studied in California.

Jones and Genoways (1967b:194) noted the complete absence of big-eared bats in Jewel Cave on 12 June 1965, and speculated that *Plecotus* vacates the cave entirely in late spring and for most of the summer. However, nets placed within the entrance to Jewel Cave on 24 July 1968 captured four *Plecotus* along with several other species (see account of *M. lucifugus*). Of the 2165 big-eared bats banded by the National Park Service at Jewel Cave from December 1959 through December 1963, nine returns have been reported. Four of these were taken within an area 30 miles south and east of Jewel Cave between elevations of 3400 and 3800 feet (see additional records) during the warm months (5 May to 1 September). The others were recaptured within the cave itself in winter. A male that was banded on 31 December 1959 was recaptured in Jewel Cave on 24 July 1968; thus, there was an interim of 3148 days between the time of banding and recapture (Turner and Davis, 1970: 364).

Of those specimens examined in Jewel Cave on 20 November 1967, 67 percent were parasitized by bat flies, *Trichobius corynorhini* Cockerell and one individual harbored a chigger, *Leptotrombidium myotis* (Ewing). Sarcoptid mites, *Sarcoptes lasionycteris* Boyd and Bernstein, were prevalent also in the Jewel Cave population. Female big-eared bats displayed a higher incidence of parasitism than did males. Two females from the maternity colony near Hot Springs, were parasitized by the same species of bat fly and by laelaptid mites, *Macronyssus longisetosus* (Furman), whereas a female from Dark Can-

yon harbored a different species of laelaptid mite, *Macronyssus unidens* Radovsky, representing the first record of this parasite in South Dakota.

One of the 22 adult females from the nursery colony near Hot Springs (obtained on 20 July 1967) was molting simultaneously over both dorsum and venter.

Specimens examined (168).—SOUTH DAKOTA: *Lawrence County:* Cleopatra Mine, 1.5 mi N Carbonate, 2 (SDMT); T. 5 N, R. 2 E, NE ¼ sec. 17, 2 (SDMT); "near Chicken Ranch and Roubaix Lake," 1 (NRW); Crowfeet [=Crow Peak?], Black Hills, 7 (AMNH); R. B. Hayes Mine, 1 (SDMT). *Meade County:* Davenport Cave, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 1. *Pennington County:* Tool Shed Cave, N Battle Creek, S Haywood, 3570 ft, 8; Rochford, 5300 ft, 1 (UMMZ); Deadman Canyon, 2-3 mi W Rapid City, 1 (NRW); Rapid City, 1 (NRW); Dark Canyon, 2 mi S, 5 mi W Rapid City, 3800 ft, 3; Spring Creek Canyon, 1 (NRW); 4 mi SW Rockerville, 5000 ft, 1 (UMMZ); Igloo Cave, 3 mi S, 16 mi W Hill City, 12 (SDMT); 3 mi SE Hill City, 3 (UMMZ); Bear Trap Cave, 4 mi S, 16 mi W Hill City, 6200 ft, 2 (1 SDMT). *Custer County:* Hell's Canyon, 13 mi W Custer, 7 (USNM); Cuyahoga Mine, 2 (SDMT); 18 mi W Custer, 1 (USNM); Jewel Cave, 2.5 mi S, 12 mi W Custer, 5280 ft, 52 (2 NRW, 3 SDMT, 1 UW, 4 WCNP); S and G Cave, T. 5 S, R. 3 E, NW ¼, NW ¼ sec. 3, 2 (SDMT); 2 mi W Wind Cave National Park, 1 (UW); Wind Cave, Wind Cave National Park, 2 (1 SDMT, 1 UW). *Fall River County:* 1 mi S, 2 mi E Hot Springs, 3400 ft, 41; 5.5 mi E Minnekahta, 4000 ft, 1.

WYOMING: *Crook County:* Sand Creek, 10 mi E Sundance, 3750 ft, 10 (USNM). *Weston County:* 4 mi E Four Corners, 1; 4 mi N, 3 mi W Newcastle, 1.

Additional records.—SOUTH DAKOTA: *Custer County:* Custer (G. M. Allen, 1916: 344); French Creek Cave, Custer State Park (R. A. Martin, pers. com.); 4 mi W Fairburn (band record: Tyers, 1963:17). *Fall River County:* 2 mi N, 1 mi W Burdock (band record); Cascade (band record); Cascade Springs (band record).

ORDER LAGOMORPHA—Hares, Rabbits, and Pikas

Family LEPORIDAE—Hares and Rabbits

Four species of lagomorphs, one of the genus *Lepus* and three of the genus *Sylvilagus*, are native to the Black Hills; two additional species of the genus *Lepus* may occur in the immediate vicinity of the Hills. The four native leporids represent interesting examples of similar species with either parapatric or sympatric, but ecologically distinct, distributions in the Hills region.

Sylvilagus audubonii baileyi (Merriam)

Desert Cottontail

Lepus baileyi Merriam, 1897, Proc. Biol. Soc. Washington, 11:148, 9 June (type locality, Spring Creek, E side Bighorn Basin, Big Horn Co., Wyoming).

Sylvilagus audubonii baileyi—Lantz, 1908, Trans. Kansas Acad. Sci., 22:236.

Nelson (1909:234) first reported the desert cottontail from the Black Hills on the basis of a young female obtained at Elk Mountain by Merritt Cary on 10 July 1906. *Sylvilagus audubonii* is a common mammal on the western Great Plains and inhabits grasslands up to about 5000 feet in the Hills. Specimens are available only from Pennington, Custer, and Fall River counties, although the species undoubtedly occurs along the entire interface of the Black Hills and surrounding prairie. The desert cottontail is geographically sympatric with the eastern cottontail and with Nuttall's cottontail; however, these three rabbits usually occupy different ecological niches.

In the western section of the Hills, Nuttall's cottontail has been collected in the same general area with the desert cottontail. Where the two occur together, *S. nuttallii* usually occurs at higher elevations in wooded or brushy habitat, whereas *S. audubonii* lives in relatively open, grassy situations at lower elevations. For example, Merritt Cary obtained both species at Elk Mountain early in the 1900's; *S. nuttallii* was taken at 6000 feet, and *S. audubonii* at 5000 feet. A similar ecological separation apparently exists between *S. audubonii* and *S. floridanus* in the eastern section of the Black Hills (see account of *S. floridanus*).

Four females taken near Minnekahta in mid-June 1967 were shot in arid grassland and pastures. Bluegrass, brome grass, cord grass (*Spartina pectinata*), western wheat grass, sagebrush, soap-

weed, pricklypear cactus, and various mustards (*Brassica* sp.) comprised the lowland vegetation. *Sylvilagus audubonii* is common in Wind Cave National Park where upland prairie is the preferred habitat. In addition to the abovementioned plants, big bluestem, little bluestem, blue grama, sideoats grama, green needlegrass, needle and thread grass, buffalo grass, yellow sweet clover, blue vervain, beardstongue (*Penstemon albidus*), wavyleaf thistle (*Cirsium undulatum*), bluestem pricklypoppy (*Argemone polyanthemos*), western wallflower (*Erysimum asperum*), blackeyed susan (*Rudbeckia hirta*), yellow coneflower (*Ratibida columnifera*), purple coneflower (*Echinacea angustifolia*), goosefoot (*Chenopodium* sp.), common sunflower (*Helianthus annuus*), scarlet globemallow (*Sphaeralcea coccinea*), wild alfalfa, woolly mullein (*Verbascum thapsus*), common milkweed (*Asclepias syriaca*), and mariposa lily clothe the prairie portion of the Park inhabited by desert cottontails.

Cranially and externally, S. *audubonii* frequently is difficult to differentiate from S. *nuttallii*. Both species have large auditory bullae and a large external auditory meatus, but in S. *audubonii* the mesopterygoid fossa and supraoccipital shield are slightly differently shaped and the pelage is somewhat paler than in S. *nuttallii*. A female cottontail from 3 mi E Custer reported by Stebler (1939:390) as *Sylvilagus nuttallii grangeri* is best assigned to *Sylvilagus audubonii baileyi*. This particular specimen is intermediate in all cranial characters, but has the paler pelage of the desert cottontail. The individual represents the greatest penetration of this species into the wooded interior of the Black Hills; however, it was taken in an area that ". . . appears to be a natural prairie, for no evidence indicating the presence of a former forest was discovered" (*loc. cit.*). Sagebrush, goldenrods, butter and eggs (*Linaria vulgaris*), and asters were conspicuous among various grasses at the site of capture.

Of four females shot southwest of Minnekahta in mid-June, one carried six embryos, another was lactating; the two others were juveniles in fresh, fine juvenal pelage. Subadult desert cottontails are present in collections made from June to September. A female taken near Custer on 16 August 1934 was in fresh summer pelage, whereas another obtained in Wind Cave National Park on 7 August 1948 was molting simultaneously over both dorsum and sides. An adult female captured at the latter locality on 1 April 1950 still was in well-worn winter pelage. An adult female and a juvenile female obtained near Minnekahta both were parasitized externally by ticks, *Haemaphysalis leporispalustris* (Packard).

Specimens examined (18).—SOUTH DAKOTA: *Pennington County:* Rapid City, 2 (NRW); Rockerville, 1 (UMMZ). *Custer County:* 4 mi E Custer, 1 (UMMZ); Buffalo Corral, Wind Cave National Park, 4300 ft, 1; Curly Canyon, 3 mi N Wind Cave, Wind Cave National Park, 1 (WCNP); 2 mi S Wind Cave, Wind Cave National Park, 2 (WCNP); Shirttail Canyon, Wind Cave National Park, 4 (UMMZ); Elk Mountain, 5000 ft, 1 (USNM). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 4; 1 mi N, 4 mi E Edgemont, 1.

Sylvilagus floridanus similis Nelson

EASTERN COTTONTAIL

Sylvilagus floridanus similis Nelson, 1907, Proc. Biol. Soc. Washington, 20:82, 22 July (type locality, Valentine, Cherry Co., Nebraska).

Sylvilagus floridanus occupies riparian communities and brushy draws across the Great Plains and into the foothill transition zone of the Black Hills. Eastern cottontails are uncommon in the Hills; they occur below 4200 feet in the eastern section, where they are sympatric with, but ecologically distinct from, S. *audubonii*. *Sylvilagus floridanus* has been reported previously from the study area as *Lepus sylvaticus* by Bailey (1888: 446), who noted that this rabbit is common in bushy ravines in the northeastern part of the Hills; however, specimens are available only from Lawrence, Custer and Fall River counties.

While a Ranger-Naturalist at Wind

Cave National Park in the summer of 1968, I had occasion to witness contrasting habitat selection between *S. f. similis* and *S. a. baileyi*. Eastern cottontails are confined to brushy draws, forest edges of valley systems that infringe into the foothills, and thickets along sides of streams; desert cottontails frequent the open prairie and upland grasslands. Several mornings were spent observing both species feeding within five feet of one another on a closely mowed lawn near Park Headquarters. To the north of the lawn was a brushy ravine of mountain mahogany, wild rose, hackberry (*Celtis occidentalis*), and chokecherry; all else was upland prairie. When startled, *S. floridanus* sought refuge in the ravine, whereas *S. audubonii* behaved much as a jackrabbit and loped off across the grassland. At the north end of the ravine is Wind Cave proper; I found the skeleton of an eastern cottontail therein on 23 August 1967. Apparently, the rabbit had been washed into the cave subsequent to a heavy rain because bones were found about 80 feet below the surface, where there was no vegetation or signs of active inhabitation by this species.

A female taken in the Park on 22 July showed no signs of reproductive activity, and a male obtained there on 31 August was a juvenile that was parasitized externally by ticks, *Ixodes spinipalpis* Hadwen and Nuttall, and chiggers, *Eutrombicula alfreddugesi* (Oudemans). Two adults, a male and a female, taken near Hot Springs in April 1950 by J. A. King, were molting over the rump.

Specimens examined (6).—SOUTH DAKOTA: *Lawrence County:* 7 mi N Spearfish, 1. *Custer County:* Wind Cave, Wind Cave National Park, 1; Headquarters, Wind Cave National Park, 4100 ft, 2. *Fall River County:* 2 mi N Hot Springs, 1 (UMMZ); 1 mi S Hot Springs, 1 (UMMZ).

Additional record.—SOUTH DAKOTA: *Pennington County:* Rapid City (Bailey, 1888: 446).

Sylvilagus nuttallii grangeri (J. A. Allen)

NUTTALL'S COTTONTAIL

Lepus sylvaticus grangeri J. A. Allen, 1895, Bull. Amer. Mus. Nat. Hist., 7:264, 21 August (type locality, Black Hills, Hill City, Pennington Co., South Dakota).

Sylvilagus nuttallii grangeri—Nelson, 1909, N. Amer. Fauna, 29:204, 31 August.

Sylvilagus nuttallii grangeri, originally described from the Black Hills, occupies areas of sagebrush and timber in the montane western United States. In the Hills, this species occurs in spruce and pine forests of the boreal cap, down through the transitional foothill zone to about 4500 feet; at the lower elevations in the western section of the Hills, forest edges and brushy draws are inhabited. In such ecotonal areas, *S. nuttallii* is sympatric with *S. audubonii*, from which it often is difficult to distinguish (see account of this species). Albeit the most abundant lagomorph in the Black Hills, specimens of Nuttall's cottontail are lacking from Meade, Fall River, and Weston counties.

I know of no instances of parapatry between *S. nuttallii* and *S. floridanus* in the study area, although such has been reported from Laramie County, Wyoming (Hall and Kelson, 1951:53). Based on the specimens examined, the nearest localities of record between these two lagomorphs in the Black Hills proper are approximately 15 miles distant [*S. floridanus* from Wind Cave National Park (4100 feet), and *S. nuttallii* from Custer (5300 feet)]. Whereas Nuttall's cottontail inhabits wooded environs above 4500 feet in the central and western Hills, the eastern cottontail occupies brushy ravines and streamside thickets below 4200 feet in the eastern Hills and along the northern and southern peripheries. Both species are distributed outward from the Hills along riparian communities on the plains, *S. floridanus* to the east and *S. nuttallii* to the west. Intergradation between *nuttallii* and *floridanus* has been suggested as possibly occurring along the eastern base of the Rocky Mountains, but Hall and Kelson (*loc. cit.*) concluded that this is not the case, partially on the basis of a study of specimens from the Black Hills.

Individuals from southeast of Hill

City, Pennington County, were collected from pine-clad uplands and spruce-filled canyons, usually near an abundance of rocks, fallen logs, shrubbery, or old buildings, all of which are in close proximity to small open grassy areas. On 7 July 1967, a melanistic juvenile which had sought refuge under a ponderosa pine log was captured on a wooded hillside near Nemo, Lawrence County.

A female obtained in Palmer Gulch, Pennington County, on 12 April 1946 carried three embryos that were 29 in crown-rump length; another taken near the same site on 13 August 1950 contained four embryos that were 17. A lactating female was captured on 10 August 1929 at Elk Mountain, and a pregnant female containing five embryos that were 56 (crown-rump) was shot northeast of Custer on 20 June 1967. Juveniles and subadults of this species are common from mid-April to early September.

The holotype, obtained on 10 August 1894 by W. W. Granger, is a nearly full-grown young of the year in subadult (post-juvenal) pelage; whereas, four paratypes are juveniles in fresh juvenal pelage, and another is an adult with worn pelage that was commencing to molt. New hairs can be observed underlying the older pelage on the rump of a topotype obtained on 25 April 1910, and on adults generally taken in June and early July. Apparently, adults molt to summer pelage from late March to mid-July, whereas change to winter pelage begins early in August on some individuals. The melanistic juvenile is entirely black except for diffuse ochraceous guard hairs over the sides, venter, and white hairs along edges of the ears and on the tail.

Specimens examined (50).—SOUTH DAKOTA: *Lawrence County:* 2 mi S Tinton, 6100 ft, 1; 2 mi W Nemo, 4700 ft, 1. *Pennington County:* Hill City, 7 (1 USNM, 6 AMNH); Redfern, 10 (USNM); Palmer Gulch, 3-4 mi SE Hill City, 5300-5400 ft, 15 (9 UMMZ); 16 mi NW Custer, 2 (UMMZ); near Mount Rushmore, 1 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 1 (FMNH); 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; Custer, 3 (USNM); Bull Springs, 2 mi N, 9 mi W Custer, 1 (UMMZ); Elk Mountain, 2 (1 USNM, 1 UMMZ); Redbird Canyon, Elk Mountain, 6000 ft, 1 (USNM).

WYOMING: *Crook County:* Devils Tower, 3 (USNM); Sundance, 1 (USNM).

Lepus townsendii campanius Hollister

White-tailed Jack Rabbit

Lepus campestris Bachman, 1837, J. Acad. Nat. Sci. Philadelphia, 7:349 (type locality, plains of Saskatchewan, probably near Carlton House).

Lepus townsendii campanius—Hollister, 1915, Proc. Biol. Soc. Washington, 28:70, 12 March, a renaming of *Lepus campestris* Bachman.

White-tailed jack rabbits inhabit upland grasslands of the northern plains and montane regions of western United States. Abundant on the surrounding flats, *Lepus townsendii* is less common in the Black Hills proper. It inhabits open woodlands up to 6000 feet and isolated grassy areas such as Reynolds Prairie, Gillette Prairie, and the Bald Hills. Although no specimens are available from Custer and Fall River counties, this species often has been observed along roads at night in these areas. Bailey (1888:438) recorded the first representatives of *L. townsendii* from the Hills (as *L. campestris*), and Palmer (1897:28, 74) indicated that a single hunter near Newcastle, Weston County, killed more than 100 individuals in 1893-94.

At lower elevations, these lagomorphs inhabit open prairie and upland grassland. I have observed them in Wind Cave National Park and in pastures just southeast of Minnekahta; in such situations *L. townsendii* overlaps ecologically with *Sylvilagus audubonii*. At higher elevations, *L. townsendii* frequents open woodlands of aspen, pine, and spruce that border meadows and pastures; under these conditions, *L. townsendii* overlaps ecologically with *Sylvilagus nuttallii* to an undetermined extent.

A female shot southeast of Hill City on 12 April 1946 contained four embryos that were 70 in crown-rump length; two males taken on 15 June 1965 and 28 June 1967 had testes that were

49 and 52 in length, respectively. Young of the year were present from mid-March to late August; in 1894 Palmer (1897:28) observed parturition of individuals at Newcastle, Wyoming, on 23 and 24 May. Specimens obtained throughout the colder months were in white pelage [V. H. Cahalane (field notes, on file at Wind Cave National Park, p. 66) observed an individual in which the change to the white winter coat was well-advanced on 3 October 1934]. The presence of new brownish hairs beneath the well-worn white hairs indicated that the pregnant female mentioned above was undergoing molt from winter to summer pelage.

A male shot southwest of Sturgis was infested with ticks, *Dermacentor andersoni* Stiles.

Specimens examined (17).—SOUTH DAKOTA: *Lawrence County:* Deadwood, 1 (USNM). *Meade County:* Fort Meade, 1 (USNM); Black Hawk, 1 (NRW); Vanocker Canyon, 7 mi S, 1 mi W Sturgis, 4800 ft, 1. *Pennington County:* Rapid City, 3 (USNM); 3.5 mi N, 1.5 mi E Deerfield, 1; Hill City, 1 (UMMZ); 3 mi SE Hill City, 5300 ft, 2 (UMMZ); 3 mi W Rockerville, 1 (UMMZ). WYOMING: *Crook County:* Devils Tower, 1 (USNM); Sundance, 6000 ft, 1 (USNM). *Weston County:* Newcastle, 3 (USNM).

ORDER RODENTIA—Rodents

Rodents are by far the most numerous of Black Hills mammals, both in number of kinds and in number of individuals. Seven families of rodents, totaling 22 species of 18 genera are indigenous to the study area; two families (represented by three genera, each of which contains but one species) have been introduced into the Hills. Four species of rodents (representing two additional genera) have been incorrectly reported from the region, and five species (representing two additional genera) may possibly occur in the Black Hills. On the basis of the numbers of individuals and resultant biomass, rodents are the base of the vertebrate food-chain in the Hills.

Family SCIURIDAE—Squirrels and Allies

Sciurids in the Black Hills represent a diversity of life forms and habits. Among terrestrial squirrels, three are fossorial (*Cynomys, Spermophilus,* and *Marmota*) and one is scansorial (*Eutamias*); two arboreal squirrels are scansorial (*Sciurus and Tamiasciurus*) and one is volant (*Glaucomys*). Except for nocturnal flying squirrels, all other taxa are diurnal and are among the most conspicuous members of the Black Hills mammalian fauna. Seasonal activity varies for the different species, some hibernate in colder months, whereas others remain active the year around.

Eutamias minimus pallidus (J. A. Allen)

Least Chipmunk

[*Tamias quadrivitatus*] var. *pallidus* J. A. Allen, 1874, Proc. Boston Soc. Nat. Hist., 16:289, June (type locality restricted to Camp Thorne, near Glendive, Dawson Co., Montana, by Cary, Proc. Biol. Soc. Washington, 19:88, 4 June 1906).

Eutamias minimus pallidus—A. H. Howell, 1922, Jour. Mamm., 3:183, 4 August.

This pale chipmunk is widely distributed in the western section of the Northern Great Plains, and inhabits riparian and scarp woodlands as well as shrubland habitats. In the Black Hills, *E. m. pallidus* occurs in the forested or brushy ravines of the lower southeastern foothills, Red Valley, and adjacent plains, at elevations up to 4300 feet. Specimens from Wind Cave National Park and from southwest of Minnekahta clearly are referrable to *pallidus,* whereas all other chipmunks examined from the Black Hills proper are assignable to the endemic race, *silvaticus* (see the following account). Distribution of *E. minimus* represents one of two examples of two subspecies of the same mammalian species occurring within the defined boundaries of the Black Hills (see account of *Dipodomys ordii*). Sutton and Nadler (1969:526) described two karyotypes (A and B) in the genus *Eutamias,* and indicated that absence of heteromorphic chromosomes is evidence that the subspecies characterized by these two different karyotypes do not intergrade. *Eu-*

tamias minimus pallidus and *E. m. silvaticus* both possess karyotype B; specimens of intermediate characteristics are encountered in the lower foothill zone, near Elk Mountain and Sundance for example.

Little ecological data are available for *E. m. pallidus* in the Black Hills region. Individuals are extremely abundant along the slopes of Wind Cave Canyon, which is vegetated by mountain mahogany, wild rose, hackberry, chokecherry, wild plum, pricklypear cactus, pricklypoppy, and soapweed. V. H. Cahalane observed this small sciurid consuming dried wild cherries and wild plums (field notes on file at Wind Cave National Park). On 29 July 1968, a female olive-backed pocket mouse captured in a snap-trap was partially devoured by a chipmunk that departed as I approached. *Perognathus fasciatus, P. hispidus, Peromyscus maniculatus, Reithrodontomys megalotis, Microtus ochrogaster* and *M. pennsylvanicus* were taken in the same trapline with *E. m. pallidus* in Wind Cave Canyon.

A male taken near Minnekahta in mid-June 1968 was molting over the rump and dorsum; scattered patches of new hair are interspersed among the older pelage on the sides and venter of another male obtained at the same time and place. Two adult females captured under these circumstances showed no sign of molt (still were in winter pelage). Molt was manifest over the shoulders and dorsum of a female collected in Wind Cave National Park on 30 August 1968.

Four placental scars were evident in the uterus of a female obtained on 13 June 1968, but three other females collected in the summer showed no signs of reproductive activity. The average length of the testes of five males collected in the summer was 7.4 (7-9).

Two males captured in Wind Cave National Park on 31 August and 1 September 1968, were parasitized externally by ticks, *Ixodes spinipalpis* Hadwen and Nuttall. Although external and cranial measurements are similar, *E. m. pallidus* differs from *E. m. silvaticus* in being paler over the upper parts, sides, and underside of tail. When compared with specimens from eight other localities in the Hills, individuals from near Minnekahta and Wind Cave National Park are significantly more pale in color tone (see Table 8). Selected external and cranial measurements of three male and four female *pallidus* from the Black Hills are: total length, 203.0±5.66, 197.0±9.80; tail length, 89.7±3.53, 75.3±12.53; hind foot length, 32.0±0.00, 32.0±0.82; ear length, 16.7±1.41, 18.4±1.89; weight, 52.9±3.96, 53.3±3.39; greatest length of skull, 32.7±0.18, 32.8±0.84; zygomatic breadth, 18.4±0.46, 18.2±0.30; braincase breadth, 15.9±0.14, 15.6±0.41; rostral length, 11.7±0.28, 11.7±0.44; interorbital breadth, 7.5±0.00, 7.0±0.53; maxillary tooth-row length, 5.2±0.04, 5.2±0.17; cranial depth, 13.3±0.14, 13.2 ±0.48.

Specimens examined (15).—SOUTH DAKOTA: *Custer County:* Beaver Creek Canyon, Wind Cave National Park, 4200 ft, 1; Elk Mountain Campground, Wind Cave National Park, 4200 ft, 1; Headquarters, Wind Cave National Park, 4100 ft, 2; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 2; Wind Cave National Park, 4 (2 UMMZ, 2 WCNP). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 5.

Eutamias minimus silvaticus White

LEAST CHIPMUNK

Eutamias minimus silvaticus White, 1952, Univ. Kansas Publ., Mus. Nat. Hist., 5:259-262, 10 April (type locality, 3 mi NW Sundance, 5900 ft, Crook Co., Wyoming).

The subspecies *silvaticus* is endemic to the Black Hills. *Eutamias minimus* is represented by three morphologically similar, but distinctively colored, races on the Northern Great Plains as follows: the dark *silvaticus* of the conifer-clad Hills, the paler *pallidus* of surrounding foothills and wooded lowland escarpments and the extremely pallid *cacodemus* of the barren alkaline topography to the east in the Badlands National Monument and vicinity (Table 8). Least chipmunks are extremely common and

TABLE 8.—Geographic variation in coloration of the mid-dorsal pelage of adult *Eutamias minimus* obtained in summer from the Northern Great Plains. Dashed lines separate populations that differ significantly.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
150 (42 ♂, 108 ♀)	*E. m. silvaticus*, Black Hills of South Dakota and Wyoming			
Mean	28.4	46.4	28.8	24.8
SD	±3.33	±0.42	±0.27	±0.28
12 (4 ♂, 8 ♀)	*E. m. pallidus*, 2 mi N, 5 mi W Ludlow, Harding Co., South Dakota			
Mean	33.0	45.2	28.8	26.0
SD	±3.39	±0.40	±0.26	±0.22
8 (6 ♂, 2 ♀)	*E. m. pallidus*, 10 m S, 5 mi W Reva, Harding Co., South Dakota			
Mean	35.8	44.2	29.7	26.1
SD	±6.90	±0.25	±0.24	±0.27
6 (3 ♂, 3 ♀)	*E. m. pallidus*, northern Campbell County, Wyoming			
Mean	36.4	45.7	28.8	25.5
SD	±3.71	±0.29	±0.25	±0.47
5 (2 ♂, 3 ♀)	*E. m. pallidus*, 0.5 m S, 1.5 m W Minnekahta, Fall River Co., and Wind Cave National Park, Custer Co., South Dakota			
Mean	39.3	45.2	29.3	25.5
SD	±3.82	±0.25	±0.11	±0.20
2 (1 ♂, 1 ♀)	*E. m. pallidus*, northern Sioux County, Nebraska			
Mean	40.0	50.6	28.8	20.6
SD	±2.12	±0.35	±0.29	±0.33
5 (1 ♂, 4 ♀)	*E. m. cacodemus*, 14 m N Long Valley, Washabaugh Co., South Dakota			
Mean	58.0	43.7	30.1	26.2
SD	±4.05	±0.25	±0.16	±0.13
4 (3 ♂, 1 ♀)	*E. m. cacodemus*, 10 m N, 4 mi E Potato Creek, Washabaugh Co., South Dakota			
Mean	69.9	44.4	30.5	25.1
SD	±9.42	±0.24	±0.14	±0.10
6 (1 ♂, 5 ♀)	*E. m. cacodemus*, 6 m S, 2 mi W Scenic, Pennington Co., South Dakota			
Mean	73.8	43.3	30.9	25.8
SD	±5.90	±0.11	±0.13	±0.13

widespread in all counties that comprise the Black Hills. Population densities seem to be much lower in the southern foothill zone and along the hogback (see account of *E. m. pallidus*). The species is most numerous in the forested uplands of the boreal cap and its presence has been noted even near the summit of

Harney Peak (7240 feet) and atop Devils Tower. *Eutamias minimus* hibernates in the colder months. Individuals inhabiting peripheral foothills and lower elevations probably hibernate for a shorter period (specimens have been taken from 9 February to 20 November in these areas) than do inhabitants of the colder recesses of the mountainous Central Basin. Least chipmunks were first reported from the Black Hills by Baird (1858: 299) under the name *Tamias quadrivittatus.*

Individuals captured in the present study either were shot or were taken in museum special snap-traps baited with rolled oats. *Eutamias minimus* apparently is ubiquitous, occurring in all habitats except extensive grasslands, which are inhabited instead by *Spermophilus tridecemlineatus.* In areas where bordering woodland interdigitates with grassland, and in campgrounds, these two small sciurids may be closely associated. Sparsely vegetated bluffs, rocky outcrops, and deteriorating abandoned buildings are environs shared with *Neotoma cinerea.* Pine-clad slopes, spruce-filled canyons, deciduous riparian woodland and brushy meadows that contain piles of logs are all inhabited by least chipmunks, which at one place or another have been obtained in association with *Sorex cinereus, Peromyscus leucopus, P. maniculatus, Reithrodontomys megalotis, Clethrionomys gapperi, Microtus longicaudus, M. pennsylvanicus* and *Zapus hudsonius. Eutamias minimus* is most conspicuous in old burned areas that are regenerating with secondary vegetative growth, and in logged areas with abundant trimmings and fallen trees. For example, from 6 to 8 September 1968, 76 individuals (39 males and 37 females) were obtained in Roby Canyon along the western edge of the Black Hills; these were taken mainly in logged areas near Roby Springs and on mountain mahogany-dominated slopes near the mouth of the Canyon.

Bailey (1888:437) noted that chipmunks in the Black Hills feed largely upon seeds of wild roses, wild rye, snowberries, asters, chokecherries, and various grasses. A male shot in Ditch Creek Valley on 14 June 1965 was carrying a juniper berry in its mouth. Reforestation programs in the Hills may suffer a 50 to 75 percent annual seed loss due to chipmunks and other small rodents (Henshaw, 1910:551); a single chipmunk was observed visiting 38 seed spots in four minutes in one experimental plot, which suffered 70 percent loss in a three-day period (Silver, 1924:167). Baits of oatmeal mixed with strychnine and water, and wheat coated with hot tallow mixed with strychnine previously have been used to control chipmunk populations in the Black Hills (Henshaw, *loc. cit.*).

White (1953b:588-589) described the process of molt in *E. m. silvaticus,* based on study of a large series of specimens taken in several seasons of the year. I concur with his general analysis. Summer molt of chipmunks in the Black Hills begins in mid-June and is completed in about mid-August. Seasonal charge in color affects mainly the tints [tone and hue], whereas the overall pattern remains constant throughout the year, and is similar in both juvenal and adult pelages (J. A. Allen, 1890:49). Comparison of pelages of 53 adults taken in June (16 males and 37 females) with 101 adults (28 males and 73 females) obtained in July indicates that the new fur of late summer reflects reds at a significantly greater intensity than does the older pelage of early summer. Measurements for the mid-dorsal region of specimens collected in June are followed by those from July: color tone, 29.5 ± 5.57, 28.3 ± 3.67; percent red reflectance, 44.7 ± 0.43, 47.2 ± 0.38; percent green reflectance, 29.7 ± 0.25, 28.4 ± 0.24; percent blue reflectance, 25.6 ± 0.27, 24.5 ± 0.26. Change in pelage is manifest either by distinct molt lines, or by interspersion of new hairs beneath the older fur. Most juvenile and subadult chipmunks obtained in the warmer months were in some stage of pelage replacement, indicating a gradual process as individuals

mature throughout the summer. Adults taken on the same day at the same locality may evidence different stages of molt, whereas others show no sign of molt. Pelage replacement may be delayed in breeding females (Howell, 1929:28). Of 70 adult females obtained in the summer that showed signs of reproduction (embryos, placental scars, or lactation), 80 percent manifested no sign of molt; the corresponding figure for 44 non-breeding adult females was 58 percent.

Of 54 adult females examined in June, 15 showed no signs of reproductive activity, 18 were lactating, 17 had an average of 5.1 (3-8) placental scars in the uteri, and four pregnant individuals carried 4.5 (3-6) embryos that were 13.7 (7-27) in crown-rump length. Twenty-four males captured in this period had testes that were 8.5 (4-17) in average length. Of fifty-seven adult females examined in July, 27 were non-breeding, 20 were lactating, 10 evinced 5.0 (3-7) placental scars, and none was pregnant. The average testicular length of 17 males collected in July was 6.1 (4-10). None of eight adult females examined in August was pregnant and reproductive activity was not evident in two of these; however, two others were lactating and 5.5 (5-6) placental scars were present in the reproductive tracts of the remaining four females of this series. The average testicular length of six males was 6.8 (6-8) in August.

Two females obtained west of Nemo on 29 June and 3 July 1967, and a male taken at Roby Springs on 7 September 1968 were parasitized externally by ticks, *Dermacentor andersoni* Stiles. Other least chipmunks captured at Roby Springs on the same date harbored another kind of tick, *Ixodes spinipalpis* Hadwen and Nuttall, lice, *Hoplopleura arboricola* Kellogg and Ferris, fleas, *Monopsyllus eumolpi* (Rothschild), and fur mites, *Dermacarus hypudaei* (Koch).

In considering geographic variation in *E. minimus*, cranial measurements were taken in the manner described by White (1953a:566) and aging criteria also followed White (1953b:587-588). There were no significant differences in dimensions of adults and old subadults, and both age groups were consolidated when making taxonomic comparisons. In contrast to the findings of White (*loc. cit.*), females were significantly larger in total body length, weight, greatest length of skull, zygomatic breadth, length of rostrum, and length of maxillary tooth-row (although absolute differences are rather small for some of these means, minor variation in a parameter that is uniformly constant will result in statistically significant differences). Therefore, sexes were treated separately when making comparisons; secondary sexual variation in coloration was not apparent.

In the Black Hills, specimens from the Bear Lodge Mountains, and western areas in general, are more reddish than individuals from elsewhere; conversely, reflection readings obtained with green and blue filters are higher for eastern populations. For example, localities in the Hills were consolidated into five groups and resultant average percent reflectance of reds for each group follows: Bear Lodge Mountains, 50.0±0.26; northwestern section, 48.0±0.32; southwestern section, 46.7±0.24; southeastern section, 44.7±0.54; and northeastern section, 42.9±0.34. Individual localities within these sections also follow this general trend. A distinct pattern of morphological variation within the Hills was not discernible. Selected external and cranial measurements of 54 males and 129 females are: total length, 194.9 ±12.82, 201.0±12.22; tail length, 81.0± 8.45, 83.3±10.27; hind foot length, 31.0 ±1.61, 31.8±4.73; ear length, 16.3±1.29, 16.1±1.55; weight, 46.8±3.89, 55.0± 6.97; greatest length of skull, 32.4±0.69, 32.6±0.48; zygomatic breadth, 18.4± 0.36, 18.6±0.39; breadth of braincase, 15.7±0.39, 15.7±0.34; rostral length, 11.4±0.30, 11.5±0.28; interorbital breadth, 7.0±0.32, 7.0±0.27; maxillary tooth-row length, 5.2±0.14, 5.3±0.15; cranial depth, 13.2±0.27, 13.2±0.23.

Specimens examined (612).—SOUTH DAKOTA: *Lawrence County:* Spearfish, 3 (SDSU); 3 mi S Spearfish, 4200 ft, 1; Whitewood, 2 (USD); Tinton, 2 mi N, 13 mi W Lead, 5900 ft, 30; 2 mi S Tinton, 6100 ft, 78; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800-6000 ft, 7; Little Spearfish Canyon, Savoy, 8 mi W Lead, 3 (USNM); 4 mi S, 7 mi W Cheyenne Crossing, 1; Deadwood, 19 (USNM); Strawberry Hill Campground, 3 mi S, 4 mi E Lead, 1 (SDMT); Dumont, 1 (USNM); Minnesota Ridge, 1 (SDSU); 2 mi W Nemo, 4700 ft, 22; Nemo, 4700 ft, 2 (1 SDSU); Blackfox Campground, 8 mi NW Rochford, 2 (NRW). *Meade County:* Vanocker Canyon, 3 mi S, 1 mi W Sturgis, 4600 ft, 1; Haven Dams, 6 mi S, 1.5 mi W Sturgis, 4600 ft, 5; 6 mi S, 1 mi W Sturgis, 4500 ft, 1. *Pennington County:* Rochford, 3 (UMMZ); South Canyon, 3-4 mi W Rapid City, 5 (AMNH); Dark Canyon, 2 mi S, 5 mi W Rapid City, 3800 ft, 9 (8 AMNH); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 50; 3 mi N, 9 mi W Deerfield, 6500 ft, 5; 3 mi N, 7 mi W Deerfield, 6900 ft, 2; Deerfield Lake, 6400 ft, 1; Castle Creek, 6500 ft, 2 (UMMZ); 2 mi S, 1 mi W Pactola, 1 (SDSU); Redfern, 5 (USNM); Sheridan Lake, 1 (SDMT); Rockerville, 16 (2 NRW, 14 UMMZ); 3 mi S, 1 mi W Rocherville, 2; 20 mi N Elk Mountain, 6000 ft, 3 (USNM); 4 mi NW Hill City, 2 (UMMZ); Ditch Creek, 14 mi W Hill City, 6400 ft, 29; Glendale, near Hill City, 19 (15 AMNH, 4 FMNH); Hill City, 4 (1 NRW, 3 USNM); 2 mi S, 13 mi W Hill City, 6400 ft, 1; 4 mi S, 16 mi W Hill City, 1; 17 mi NW Custer, 1 (UMMZ); 16 mi NW Custer, 53 (UMMZ); Palmer Gulch, 3-4 mi SE Hill City, 5300-5400 ft, 20 (UMMZ); Horse Thief Lake, 3 mi W Mount Rushmore National Monument, 5100 ft, 1; unspecified locality, 5 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 5 (FMNH); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 15; 5.75 mi N, 5.75 mi E Custer, 5200 ft, 22; Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 12; Roby Canyon, 2 mi N, 22 mi W Custer, 5200 ft, 4; Bull Springs, 2 mi N, 9 mi W Custer, 6500 ft, 8 (UMMZ); 0.9 mi W Custer, 1 (SDMT); Custer, 5300 ft, 13 (4 AMNH, 2 UMMZ, 7 USNM); Bismark Lake Campground, 1 mi E Custer, 1 (SDMT); 4 mi SW Custer, 3; Squaw [=Grace Coolidge] Creek, 1 (AMNH); Custer State Park, 21 (UMMZ); Campbell's Ranch, Elk Mountain, 4800 ft, 5 (1 UMMZ, 4 USNM); Mayo, 1 (USD); 3 mi SW Pringle, 2; unspecified locality, 5 (4 UMMZ, 1 USD).

WYOMING: *Crook County:* Devils Tower, 4 (USNM); Warren Peak, Bear Lodge Mountain, 6000 ft, 3 (USNM); 15 mi N Sundance, 5500 ft, 6; 15 mi ENE Sundance, 3825 ft, 1; 3 mi NW Sundance, 5900 ft, 17; 1 mi N Sundance, 1; Sundance, 8 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 19; 4 mi E Four Corners, 6; 9 mi N, 1 mi E Newcastle, 2; 6 mi N Newcastle, 1; Newcastle, 3 (USNM); SE Newcastle, 1 (USNM).

UNSPECIFIED LOCALITY. Black Hills, 4 (2 AMNH, 2 SDSU).

Additional records.—SOUTH DAKOTA: *Pennington County:* Rapid City (Howell, 1929: 57). WYOMING: *Crook County:* 2.5 mi N Sundance (Sutton and Nadler, 1969:526).

Marmota flaviventris dacota (Merriam)

Yellow-bellied Marmot

Arctomys dacota Merriam, 1899, N. Amer. Fauna, 218, 30 October (type locality, Black Hills, Custer, Custer Co., South Dakota).

M[armota]. f[laviventer]. dacota—A. H. Howell, 1914, Proc. Soc. Washington, 27:15, 2 February.

[*M.*] *flaviventris dacota*—A. H. Howell, 1915, N. Amer. Fauna, 37:7, 7 April.

Yellow-bellied marmots are distributed in montane areas of the western United States, being confined to mountains, foothills and rocky canyons, and not occurring on the plains proper. Baird (1858:344) first noted the occurrence of this marmot in the Black Hills, as *Arctomys flaviventer*. The subspecies *dacota* is named from, and restricted to, the Black Hills of South Dakota and Wyoming, where it inhabits rocky hillsides, crevices in bluffs, rockpiles in meadows, or abides beneath deserted buildings. Altitudinal distribution is from the boreal cap of the Hills, down to about 4000 feet. Specimens of this species have been recorded from all counties that comprise the study area. Yellow-bellied marmots hibernate during the colder months; the earliest and latest seasonal records from the Hills known to me are 12 April and 22 August, respectively.

Distribution of *Marmota flaviventris* in the Hills coincides with the occurrence of rocky outcroppings or other high vantage points from which these animals can sun themselves and survey the surrounding countryside. These vantage points are closely associated with montane meadows, pastures, and fields of alfalfa and clover. Vernon Bailey found flowers, leaves, and green seeds of various plants, including milk-vetch (*As-*

tragalus bisulcatus) and stonecrop (*Sedum douglasii*) in the stomachs of marmots from the Black Hills (Howell, 1915:13).

Specimens from Ditch Creek Valley, Beaver Creek Valley, and Little Spearfish Canyon generally were taken in habitats as described above. An adult female and seven juveniles (four females and three males) obtained southwest of Keystone were shot at the entrance of an old lead-zinc mine and in adjacent woodpiles. The mine was on a hillside that was clad in pine and bur oak; well-used pathways were evident leading from the mine to a valley meadow of bluegrass and clover below.

A field party from The University of Kansas dug an adult female and six young males out of a den in Reuter Canyon on 4 July 1947. The burrow was in a hillside that faced north and the tunnel ran obliquely upward about 10 degrees from the horizontal for approximately 12 feet, leveled off and ran at a right angle for another six feet; no nest was located.

A graduate student from the Museum of Natural History, Paul B. Robertson, spent several days observing a colony of yellow-bellied marmots (five adults and seven juveniles) at a locality 4 mi W Nemo, Lawrence County. The colony occupied an area of about 500 square yards that comprised an old homestead. Deserted buildings, rock piles, and woodpiles were situated in a meadow and a pasture. Activity of the marmots began about 6:45 hrs (MDT) on sunny mornings, with more restricted activity on cloudy days. After an initial period of vigilance, marmots spent most of the morning grazing on the meadow. Movement of adults was much more conservative than that of the young; while adults remained alert, young romped freely, stopping often to preen or graze. When feeding in tall grass, marmots raised up on their haunches much more frequently than in short grass, and feeding was more sporadic. In late morning and early afternoon, grazing activity declined and sunning behavior increased. On one occasion, the colony sensed the approach of a man while he was yet one-quarter of a mile distant. After a series of whistles from the adults, young animals retreated toward the burrow systems, while the older marmots remained alert until the man passed from sight. Grazing activity increased once again about 16:30 hrs (MDT) and continued until near dusk.

Two pregnant females obtained southeast of Hill City on 12 April 1946 contained five and six embryos that were 16 and 9 in crown-rump length, whereas a female from near Keystone (22 June 1967) and another from Little Spearfish Canyon (1 August 1967) evidenced eight and two placental scars, respectively. Lactating females were taken on 13 and 22 June 1967, and on 8 July 1965; young marmots were common from early July through August. Testicular length of an adult male collected on 12 June 1965 was 12, and testes of six subadult males captured early in August 1967 had an average length of 8.2 (7-10).

The venter, feet, tail, and underfur of juveniles from near Keystone are a dull dark brown, with a pale brown- or beige-tipped guard hairs over the dorsum and sides, in contrast to the brightly colored reddish hairs of adults. Change from subadult to adult pelage and annual molt in adults occurs from mid-June through July. Replacement of the old pelage is most noticeable over the mid-dorsum, sides, and rump; replacement of the mantle (a cloak of long hairs covering the shoulders and anterior third of the dorsum) is more difficult to observe but on occasion new hairs are evident. The adult female from near Keystone seemed to have a mange-like disease and lacked hair entirely over the mid-dorsum.

Marmota flaviventris dacota differs from *M. f. luteola* of south-central Wyoming (Converse, Albany, and Carbon counties), in the greater contrast in color between the mantle and mid-dorsal pelage (Table 9) and brighter color of the mantle of the former. Howell (1915:50)

TABLE 9.—Geographic variation in coloration (mean and standard deviation) of the mantle and mid-dorsal pelage of adult *Marmota flaviventris* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
13 (4♂, 9♀)	*M. f. dacota*, Black Hills of South Dakota and Wyoming			
Mantle	51.4±8.59	54.9±0.23	25.3±0.16	19.8±0.10
Dorsum	36.3±5.40	53.1±0.75	23.9±0.39	23.0±0.42
8 (2♂, 6♀)	*M. f. luteola*, south-central Wyoming			
Mantle	39.9±6.89	54.2±0.30	25.9±0.29	19.9±0.24
Dorsum	32.8±5.59	56.8±0.59	23.1±0.36	20.1±0.26
10 (2♂, 8♀)	*M. f. nosophora*, western Wyoming			
Mantle	50.3±11.66	50.3±0.36	26.1±0.34	23.6±0.23
Dorsum	34.3±5.44	51.3±0.53	25.3±0.14	23.4±0.48

noted that *dacota* is the brightest of all races of the species, with red and yellow shades being most pronounced and blacks and browns reduced to a minimum. Indeed, along with that of *Tamiasciurus hudsonicus*, pelage of yellow-bellied marmots reflects reds at greater intensities than that of other species examined from the Black Hills. *Marmota flaviventris luteola* also lacks the blackish muzzle of *M. f. dacota*, and has somewhat smaller average dimensions; total body length (577.5±36.45) and interorbital breadth (17.7±1.41) of two male and six female *luteola* differ significantly from those of six male and 10 female *dacota* (620.7±47.06 and 20.3±2.06, respectively). Intergradation between these two subspecies is evident in specimens from the Laramie Mountains, where individuals are more reddish in color and the total body length and interorbital breadth are greater than in typical *luteola*.

Marmota flaviventris nosophora of western Wyoming (Park, Big Horn, Washakie, Sublette, Fremont and Natrona counties) is similar to *dacota*, but has slightly smaller average dimensions; the upper parts differ significantly in reflection of reds, are slightly darker in tone, and are more mixed with black; the mantle of *nosophora* reflects blues at significantly greater intensities than that of either *dacota* or *luteola* (Table 9). Specimens similar to each of the three subspecies can be found in south-central Wyoming due to intergradation and the high degree of individual variation in yellow-bellied marmots of that area (Long, 1965:568).

Significant secondary sexual differences in color and size of *M. f. dacota* are not apparent, nor is a pattern of variation within the Black Hills readily discernible. Selected external and cranial measurements of six males and 10 females from the Hills are: total length, 620.7±47.06; tail length, 178.7±24.52; hind foot length, 79.9±3.54; ear length, 29.3±6.32; weight (kilograms), 3.0±0.83; greatest length of skull, 84.3±3.73; zygomatic breadth, 55.9±2.73; rostral length, 33.8±2.04; interorbital breadth, 20.3±2.06; postorbital breadth, 16.9±0.93; mastoid breadth, 40.6±1.99; and length of maxillary tooth-row, 20.9±0.61.

Specimens examined (73).—SOUTH DAKOTA: *Lawrence County:* Tinton, 2 mi N, 13 mi W Lead, 5900 ft, 4; Little Spearfish Canyon, Savoy, 5 (USNM); Little Spearfish Canyon, 1 mi S, 9 mi W Lead, 5400 ft, 4; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 4; 3 mi W Nemo, 4800 ft, 1; 1 mi E Nemo, 4700 ft, 1. *Meade County:* Vanocker

Canyon, 6 mi S, 1 mi W Sturgis, 4500 ft, 2. *Pennington County:* Beaver Creek Valley, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 2; Dark Canyon, 2 mi S, 5 mi W Rapid City, 1 (AMNH); Sheridan Lake, 6 mi NNW Keystone, 1; 5.4 mi E Mount Rushmore National Monument, 1 (SDMT); Ditch Creek Valley, 14 mi W Hill City, 6400 ft, 7; Tigerville, 1 (USNM); Palmer Gulch, 3 mi SE Hill City, 5300 ft, 2 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5400 ft, 1 (FMNH); 3.3 mi S, 0.5 mi W Keystone, 5000 ft, 8; Custer, 13 (7 USNM, 6 AMNH); Doran's Ranch, 3 mi E Custer, 1 (UMMZ). *Fall River County:* 5.5 mi E Minnekahta, 4000 ft, 1.

WYOMING: *Crook County:* Reuter Canyon, 1 mi S Warren Peak, 6000 ft, 8; Bear Lodge Mountains, 1 (USNM). *Weston County:* 0.5 mi E Buckhorn, 6100 ft, 1; 1.5 mi E Buckhorn, 6150 ft, 1.

UNSPECIFIED LOCALITY: Black Hills, 2 (1 USNM, 1 FMNH).

Spermophilus tridecemlineatus pallidus J. A. Allen

THIRTEEN-LINED GROUND SQUIRREL

Spermophilus tridecem-lineatus var. *pallidus* J. A. Allen, 1874, Proc. Boston Soc. Nat. Hist., 16:291, June (nomen nudum).

Spermophilus tridecemlineatus var. *pallidus* J. A. Allen, 1877, *in* Coues and Allen, Bull. U. S. Geol. Surv. Territories, 11:872, August (type locality restricted to the mouth of the Yellowstone River, McKenzie Co., North Dakota, by A. H. Howell, N. Amer. Fauna, 56:122, footnote, 18 May 1938).

Spermophilus tridecemlineatus olivaceus J. A. Allen, 1895, Bull. Amer. Nat. Hist., 7:337, 8 November (type locality, Black Hills, Custer, Custer Co., South Dakota).

The thirteen-lined ground squirrel inhabits dry grasslands of the central United States, and is locally common within the Black Hills in areas of short grass such as moderately grazed pastures, mowed borders of roadways and campgrounds, and upland meadows. This spermophile ranges through the foothill transition zone up to 6500 feet, but is more common below 5500 feet. *Spermophilus tridecemlineatus* hibernates in the study area from mid-September until early April; the earliest and latest seasonal records as evidenced by the specimens examined are 8 April and 7 September, respectively.

Grinnell (1875:82) observed large numbers of this species on the surrounding plains, but saw none while in the Black Hills; S. *tridecemlineatus* was first noted therein by Bailey (1893:45). Ground squirrels often are observed during the day along roadsides and in the parkways of campgrounds. Traps placed in these areas took five specimens in Ditch Creek Valley in mid-June 1965; another was shot as it ran from its burrow after water was poured into the tunnel system. In Wind Cave National Park, two individuals were taken on 27 August 1968 along a fence that served as a corral for bison. The enclosed area was closely grazed, whereas exterior to the fence, natural prairie grasses and forbs were about knee-high. J. A. King obtained several S. *tridecemlineatus* in early April in an upland meadow that was being grazed by horses; one individual was carrying unidentified seeds in its cheeks. Fifty percent of the stomach contents of a female taken at Custer in July 1893 was composed of grasshoppers and other insects, the remainder being seeds and vegetable matter (Bailey, 1893).

Reithrodontomys megalotis, *Peromyscus maniculatus*, *Microtus ochrogaster*, and *Eutamias minimus* often were taken in the same trapline with the thirteen-lined ground squirrel. Long (1965:581) stated that he had seen *Spermophilus tridecemlineatus* and *Eutamias minimus* "so closely associated in Custer County, South Dakota, that the latter could be chased into the burrows of the former."

Four of eight females (for which reproductive data are available) taken from 12 June to 1 July, were pregnant, averaging 7 (3-9) embryos that were 17 (6-27) in crown-rump length; another individual was lactating. Testes of five males obtained in the same period were 10.4 (5-16) in length. Juveniles first appeared above ground in early July, and were common by mid-summer.

Seven individuals obtained in mid-June west of Hill City were molting conspicuously over both sides and the dorsum. A female from Wind Cave National

Park harbored several ticks, *Ixodes sculptus* Neumann, and fleas, *Thrassis fotus* (Jordan).

J. A. Allen (1895b:337) described a new subspecies, *Spermophilus tridecemlineatus olivaceus* from the Black Hills; he indicated that it differed from the nearby *pallidus* "in its much darker ground color and the olivaceus creamy white tint of the light stripes and spots." A. H. Howell (1938:113) placed *olivaceus* in the synonomy of *pallidus*, stating: "The type series of *olivaceus* from Custer, South Dakota, has been compared with a large series of typical *pallidus* and is found to agree closely with it." Long (1965:581) reinstated *olivaceus* as a subspecies of *S. tridecemlineatus*, indicating that in addition to the difference in coloration noted by Allen, *olivaceus* also is characterized by shorter nasals, larger auditory bullae, and longer external ears than *pallidus*.

I have compared a large series of specimens from the Black Hills with typical *pallidus* from northwestern (Harding County) and southwestern (Bennett County) South Dakota, northern and western Nebraska (Sioux, Cherry, Keya Paha, and Cheyenne counties), northeastern Wyoming (Campbell, and Weston counties), and southeastern Wyoming (Albany, Goshen, and Laramie counties). Morphologically, spermophiles from the Black Hills fall within the range of variation of the comparative material and do not differ significantly from *pallidus* in any dimension (Table 10).

Ground color and coloration of stripes and spots on individuals of *S. tridecemlineatus* vary greatly, and most possible color combinations are present when a large series of specimens is examined. On the average, mid-dorsal pelage of thirteen-lined ground squirrels from the

Table 10.—Geographic variation in selected external and cranial measurements of adult *Spermophilus tridecemlineatus* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Ear length	Greatest length of skull	Zygomatic breadth	Rostral length	Length of maxillary tooth-row	Skull depth	Greatest diameter of auditory bullae
21 (10♂, 11♀)			Black Hills, South Dakota and Wyoming					
Mean	232.1	9.1	38.5	22.5	14.8	7.2	16.7	8.4
SD	±7.44	±1.64	±1.08	±0.86	±0.63	±0.33	±0.39	±0.33
4 (1♂, 3♀)			Harding County, South Dakota					
Mean	241.2	8.0	38.3	23.7	15.0	7.2	16.4	8.2
SD	±13.74	±1.41	±0.60	±0.65	±0.47	±0.31	±0.07	±0.32
3 (1♂, 2♀)			Bennett County, South Dakota					
Mean	242.7	9.0	39.5	23.3	15.5	7.3	16.5	8.5
SD	±11.68	±1.00	±0.64	±0.12	±0.35	±0.29	±0.26	±0.00
7 (2♂, 5♀)			Northeastern Wyoming (see text)					
Mean	223.7	9.7	37.6	22.3	14.3	6.9	15.8	8.1
SD	±19.39	±1.03	±1.38	±0.94	±0.73	±0.28	±0.61	±0.12
11(5♂, 6♀)			Southeastern Wyoming (see text)					
Mean	228.9	7.2	38.1	22.5	15.1	7.0	16.4	7.9
SD	±16.33	±1.32	±1.27	±0.79	±0.68	±0.18	±0.61	±0.33
5 (2♂, 3♀)			Northern and western Nebraska (see text)					
Mean	246.0	9.4	38.9	23.6	15.3	7.4	16.7	8.4
SD	±6.68	±1.52	±1.91	±1.07	±0.74	±0.28	±0.36	±0.17

Hills is dark in tone, high in reflectance of reds, and low in reflectance of blues (Table 11). However, these individuals readily fall within the range of variation of populations from Bennett County and from parts of Wyoming, and do not differ significantly from them. Thus, I must concur with Howell and place *S. t. olivaceus* in the synonomy of *S. t. pallidus*.

Significant secondary sexual variation was not evident. Although males averaged somewhat larger in several cranial dimensions, females were slightly larger in total length and length of tail. Additional measurements (not listed on Table 10) of 31 *S. t. pallidus* from the Black Hills are: tail length, 75.3±7.16; hind foot length, 31.5±1.40; weight, 111.5± 22.73; and postorbital breadth, 11.1± 0.57.

Specimens examined (102).—SOUTH DAKOTA: *Lawrence County:* 1.5 mi S, 0.5 mi E Spearfish, 3800 ft, 1; Crowfeet [=Crow Peak?], Black Hills, 1 (AMNH). *Meade County:* Black Hawk, 1 (AMNH). *Pennington County:* 0.5 mi N Silver City, 1 (SDMT); Rapid City, 2 (NRW); Beaver Creek Valley, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 1; Ditch Creek Valley, 14 mi W Hill City, 6400 ft, 6; 2 mi S, 13 mi W Hill City, 1; Pactola, 1 (USNM); Castle Creek, 6500 ft, 2 (UMMZ); Diamond S Ranch, near Rapid City, 2 (UMMZ); Palmer Gulch, 3-4 mi SE Hill City, 53-5400 ft, 7 (UMMZ); unspecified locality, 1 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 4 (FMNH); Harney National Forest, 10 (UMMZ); Custer, 25 (1 UMMZ, 18 AMNH, 4 USNM, 2 FMNH); Bull Springs, 2 mi N, 9 mi W Custer, 10 (USNM); Elk Mountain, 1 (USNM); Buffalo Corral, Wind Cave National Park, 4300 ft, 2; Wind Cave National Park, 2 (WCNP).

WYOMING: *Crook County:* Bear Lodge Mountains, 5200 ft, 1 (USNM); 15 mi N Sundance, 5500 ft, 3; 1.5 mi NW Sundance, 5000 ft, 6; 1 mi N Sundance, 1; Sundance, 5 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 4; Newcastle, 1 (USNM).

TABLE 11.—Geographic variation in coloration of the mid-dorsal pelage of adult *Spermophilus tridecemlineatus* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
21 (10♂, 11♀)		Black Hills, South Dakota and Wyoming		
Mean	33.8	47.3	28.9	23.8
SD	±8.30	±0.17	±0.10	±0.09
4 (1♂, 3♀)		Harding County, South Dakota		
Mean	45.0	45.3	30.1	24.6
SD	±6.89	±0.22	±0.11	±0.15
3 (1♂, 2♀)		Bennett County, South Dakota		
Mean	32.8	47.2	28.4	24.4
SD	±4.65	±0.32	±0.12	±0.19
7 (2♂, 5♀)		Northeastern Wyoming (see text)		
Mean	41.9	45.4	30.2	24.4
SD	±4.74	±0.14	±0.17	±0.09
11 (5♂, 6♀)		Southeastern Wyoming (see text)		
Mean	47.4	45.6	29.2	25.2
SD	±5.36	±0.16	±0.18	±0.14
5 (2♂, 3♀)		Northern and western Nebraska (see text)		
Mean	49.5	45.5	29.7	24.8
SD	±6.09	±0.17	±0.11	±0.07

Cynomys ludovicianus ludovicianus (Ord)

Black-tailed Prairie Dog

Arctomys ludoviciana Ord, 1815, *in* Guthrie, A new geogr., hist., coml. grammar . . ., Philadelphia, Amer. ed. 2, 2:292, description on page 302 (type locality restricted to the "Tower," sec. 10, T. 34 N, R. 10 W, Boyd Co., Nebraska, by Jones, Univ. Kansas Publ., Mus. Nat. Hist., 16:140, 1 October 1964).

Cynomys ludovicianus—Baird, 1858, Mammals, *in* Repts. Expl. and Surv. . ., 8(1):331, 14 July.

The black-tailed prairie dog is a characteristic inhabitant of the short-grass plains of central United States. F. V. Hayden (1862:145) first noted this species in the Hills region: "The largest one [prairie dog town] I have seen is near the Black Hills, north of the Big Sheyenne river [Cheyenne River]. This village, though sometimes interrupted by high ridges or hills is connected, and covers an area of over fifty square miles." The Shirttail Canyon prairie dog town in the southwest corner of Wind Cave National Park was studied extensively by J. A. King (1955). C. B. Koford (1958) also studied the Shirttail Canyon colony, as well as the prairie dog town in Devils Tower National Monument. These two reports were consulted frequently in preparing the present account. Bailey (1888:440-441) described a prairie dog colony that occupied about 40 acres at a place 2 mi E Rapid City.

The Devils Tower prairie dog town comprises about 40 acres between the Belle Fourche River and the pine-clad hills of the National Monument. The town is at least 75 years old; in June 1894, Vernon Bailey noted "a good sized dog town occupies a level section in the valley at base of tower" (USBS files). Counts made in 1947 and 1955 indicated that the population was fairly stable at about 750 prairie dogs. In the area where *Cynomys* are fed by tourists, the number of burrows reaches a maximum density of 100 per acre.

The Shirttail Canyon prairie dog town occupies about 75 acres, covering part of the canyon floor and adjacent terraces. In 1950, King counted 614 burrows on an 11.7 acre sample plot of this town (52.5 per acre). Wind Cave National Park supports seven naturally established prairie dog towns and three new ones that were initiated in the northwesternmost corner of the Park in 1965. *Cynomys ludovicianus* occupies about 655 acres, or three percent of the nonforested portion (21,449 acres) of the Park. Total acreage inhabited by prairie dogs increased by 90 acres from 1963 to 1967.

This species is active the year around, although activity decreases somewhat during the colder months and on cloudy days. Both King and Koford found that males lose more weight than females during winter, possibly indicating that males are more active at that time. Burrows are constructed on floors of canyons and on adjacent terraces, where fine-textured chernozems and chestnut soils enable prairie dogs to excavate deep, continuous passages; at Devils Tower, many burrows were located in fine sand of the Belle Fourche River floodplain. Barriers to expansion of prairie dog towns seem to be unsuitable soils of adjacent slopes, heavy cover, and rough terrain.

Earthen mounds thrown up around the entrances to burrow systems favor establishment of pioneer forbs such as bigbract verbena (*Verbena bracteata*), stickweed (*Lappula redowskii*), dogweed (*Dyssodia papposa*), and false pennyroyal (*Hedeoma hispida*). Koford analyzed the vegetation along a transect through the Shirttail Canyon colony and found that the center of the town supported 67 percent buffalo grass, 24 percent tumblegrass (*Schedonnardus paniculatus*), six percent blue grama, and three percent western wheat grass. In the peripheral area, blue grama and western wheat grass increased in abundance and the town border was dominated by Japanese brome grass (*Bromus japonicus*). Within the confines of a town, prairie dogs usually cut down tall plants

that otherwise would obstruct a clear field of observation; examples of such plants are woolly mullein, Russian thistle (*Salsola kali*), snowberry (*Symphoricarpos occidentalis*), silver sagebrush, and brome grass. Other species such as snow-on-the-mountain (*Euphorbia marginata*), clammyweed (*Polanisia graveolens*) and various mustards are left erect, presumably due to a bitter taste, presence of thorns, a tough integument, or other protective devices of the plants. In addition to the numerous plant species listed by King (1955:8 and 9), Koford included scarlet globemallow, cutleaf nightshade (*Solanum triflorum*), pepperweed (*Lepidium densiflorum*) and lamb's-quarters as important foods of *Cynomys ludovicianus* in the Black Hills region.

King reported that the Shirttail Canyon colony was divided into fairly stable social groups of several members, each group occupying a particular territory of approximately one acre in size and each consisting of an adult male with a few females and their young. Even though a mother prairie dog defends the area of her nest burrow, Koford thought it was improbable that this aggressiveness limits the number of families; for example, 11 nest burrows were found in an area of only 1.5 acres in Shirttail Canyon.

Expansion of a dog town presumably occurs when the population density increases shortly after the pups emerge from below ground. King noted that emergence of pups in May raised the average population density from four to 15 prairie dogs per acre. In contrast to the behavior of most rodents, adult prairie dogs move into a new area, from which the young are repulsed. The longest movement recorded by King was 800 feet beyond the edge of the colony. Search for food may be another cause of colony expansion.

In early July 1968, I observed an adult badger and two young excavating a prairie dog burrow in Wind Cave National Park early in the morning. Several burrows in Shirttail Canyon also were dug out by badgers, and coyotes are a fairly common sight in towns early in the morning. Although no actual sightings have occurred since 1953, characteristic trenches of the black-footed ferret were found in the National Park in 1969. King reported that a prairie dog was killed by a golden eagle in the winter of 1955; I observed an eagle swoop down upon an adult prairie dog in the summer of 1968, but the prairie dog escaped into its burrow. Remains of a young *C. ludovicianus* were found in pellets of a great horned owl that was roosting in Wind Cave Canyon in July 1968.

Mating occurs in February and March and two to 10 young are born in early April after a gestation period of 30 to 35 days. The pups emerge from under ground in mid-May. Evidently, only one litter is produced per year. King found no evidence of reproduction among yearlings and noted that mortality was high in the young during the first (36%) and second (22%) years.

King noted that fleas (*Opisocrostis hirsutus*), mites (*Atricholaelaps glasgowi*), and ticks (*Ixodes* sp.) parasitize prairie dogs externally in Shirttail Canyon.

Specimens examined (29).—SOUTH DAKOTA: *Pennington County:* 0.5 mi E Rapid City, 1 (SDSU); Rapid City, 11 (USNM). *Custer County:* McAdam's Ranch, 3 mi NW Wind Cave, 1 (WCNP); Wind Cave National Park, 5 (2 UMMZ, 2 UW); Elk Mountain, 5 (UMMZ); 1 mi NE Wind Cave, Wind Cave National Park, 2 (WCNP).

WYOMING: *Weston County:* Newcastle, 4 (USNM).

Additional records.—SOUTH DAKOTA: *Meade County:* Sturgis (USBS files). *Custer County:* Pringle (USBS files); Horseshoe Bend, 12 mi NE Elk Mountain (USBS files).

Sciurus niger rufiventer

É. Geoffroy St.-Hilaire

Fox Squirrel

Sciurus rufiventer É. Geoffroy St.-Hilaire, 1803, Catalogue des mammifères du Museum National d'Histoire Naturelle, Paris, p. 176 (type locality restricted to Mississippi Valley, probably between southern Illinois and

central Tennessee, by Osgood, Proc. Biol. Soc. Washington, 20:44, 18 April 1907).

Sciurus niger rufiventer—Osgood, 1907, Proc. Biol. Soc. Washington, 20:44, 18 April.

The fox squirrel is a common resident of timbered areas and urban communities of eastern and central South Dakota, but has been reported in Wyoming only from Cheyenne and Laramie (Long, 1965:598) and from the Black Hills (Maxwell and Brown, 1968:155). The distribution of this species in western South Dakota is essentially dendritic along the major river systems; for example, throughout the valley of the White River. In the Hills, the distribution of *Sciurus niger* characteristically follows that of the bur oak and other deciduous elements, particularly on many slopes that lead up from stream beds in the northern Hills and the Bear Lodge Mountains, and in wooded ravines of the foothill zone.

Spread of the fox squirrel in Nebraska (Jones, 1964:146) and North Dakota (Hibbard, 1957:527) has been well documented. This species probably would not occur in the study area were it not for the occurrence of gallery forests along river systems across the plains that served as avenues of dispersal and for introduction by man. I know of no introductions into the Black Hills proper, but fox squirrels are known to have been introduced in some adjacent areas (northwestern Nebraska, for example; see Jones, 1964).

Hayden (1856:79) indicated that the nothernmost limit of the fox squirrel in the plains region was at the mouth of Running Water [Niobrara River] on the Missouri, but later (1859:708) noted that this species reached the limits of its range at the mouth of the White River. I have observed these sciurids in residential areas in Spearfish, Rapid City, and Hot Springs, and I have heard the distinctive bark of fox squirrel in Beaver Creek Canyon in Wind Cave National Park. Residents report this squirrel as being quite common along wooded streams east and north of Spearfish.

Specimens examined (5).—SOUTH DAKOTA: *Pennington County:* Rapid City, 3 (1 SDMT, 2 NRW); 0.75 mi SW Rapid City, 1 (SDSU).

WYOMING: *Crook County:* Sand Creek, S Beulah, 1 (UW).

Tamiasciurus hudsonicus dakotensis (J. A. Allen)

Red Squirrel

Sciurus hudsonicus dakotensis J. A. Allen, 1894, Bull. Amer. Mus. Nat. Hist., 6:325, 7 November (type locality, Squaw [=Grace Coolidge] Creek, Custer Co., South Dakota).

Tamiasciurus hudsonicus dakotensis—Hayman and Holt, 1940, *in* Ellerman, The families and genera of living rodents, British Mus., 1:346, 8 June.

In the northern plains region, *Tamiasciurus hudsonicus* inhabits montane forests and several scattered conifer-clad escarpments. The species is commonest on the boreal cap of the northern Black Hills where both white spruce and ponderosa pine are predominant; the former conifer is scarce in the drier southern woodlands, and accordingly, population densities of *Tamiasciurus* are much lower in these areas. The red squirrel, or chickaree, is found in the Hills at elevations above 3800 feet, but is most numerous above 5200 feet.

Hayden (1859:708) first reported *T. hudsonicus* from the Black Hills, and J. A. Allen (1894a:325) later described *dakotensis* is an endemic subspecies (see Hall and Kelson, 1959:400, map 257). However, *dakotensis* is not restricted to the Hills, but occurs also in several outlying areas. For example, Vernon Bailey captured a female at Belle Fourche, Butte Co., South Dakota, on 21 October 1887. B. W. Evermann obtained a male at Edgemont, Fall River Co., South Dakota, on 7 October 1892, and V. H. Cahalane took a male 5 mi S Hermosa, Custer Co., South Dakota, on 12 December 1934. J. A. Allen (1877:689) reported a specimen from Bear Buttes, Meade Co., South Dakota. W. J. Hoffman (1877:97) noted that this species "sometimes is found in oak groves eight miles west of the Post [Grand River Military Post, Corson Co.,

South Dakota]," but this report is open to question. Swenk (1908:81) and Visher (1914:88) noted the former distribution of red squirrels in northern Nebraska and Harding County, South Dakota, respectively; however, Jones (1964:337-338) did not admit *Tamiasciurus* to the fauna of Nebraska, and Andersen and Jones (1971:375) reported that the species evidently does not now occur in Harding County, although they did record a specimen from the Long Pine Hills in adjacent Carter County, Montana, as *dacotensis*. Specimens of *T. hudsonicus* tentatively assigned to *dakotensis* have been reported from southeastern Montana and the northern Laramie Mountains in Wyoming (Hoffman and Jones, 1970:374, Fig. 7).

This sciurid is active in the Hills the year around. Although this species does not hibernate, it may undergo periods of quiescence during prolonged inclement weather. A few individuals can be observed in summer at most hours of the day, but maximal activity occurs between 7:00 and 9:30 hrs (MDT) and from 16:30 hrs to dusk. Even though population densities vary from area to area, the red squirrel is ubiquitous in wooded environs; pine-clad slopes, spruce-filled canyons, and oak-bordered drainage systems all are inhabited. In the latter habitat, *Tamiasciurus* is ecologically sympatric with *Sciurus niger* to an unknown extent. The fox squirrel is far less common and its distribution in the Hills closely approximates that of bur oak and other deciduous elements.

While with a Museum of Natural History field party in 1947, R. B. Finley studied several external nests (located on branches of trees, rather than in a den cavity) of red squirrels in Crook County, Wyoming. He located three ponderosa pine nest trees on a 30° slope with a southeastern exposure; the trees were from eight to 17 inches in diameter, and 30 to 60 feet in height. Nests were built 22.3 (18 to 25) feet above the ground and either were placed adjacent to the trunk, or rested upon a horizontal limb (two to four inches in diameter) within two feet of the trunk. The loosely constructed nests were roughly oval in shape, measuring 15 (13 to 17) inches in length, 11.3 (9 to 13) inches in width, and 7.3 (6 to 8) inches in depth. Interiors of the nests were shapeless, unlined spaces, lacking a well-defined nest chamber. These were temporary or summer nests, but characteristic winter nests are tightly constructed of twigs, lichens, mosses and other plant materials, and frequently were observed among the dense foliage of white spruce in the northern Black Hills.

Materials used in construction of summer nests were varied, consisting of newspaper scraps (probably from a nearby abandoned Civilian Conservation Corps Camp), shredded cloth and bark, tufts of fur, and particles of lichens and dried graminoid plants. Another member of the field party, E. P. Marks, examined two of the above nests and found 18 dipteran larvae, three dipteran pupae, five flea larvae, two unidentified fleas, one pseudoscorpian and eight collembolans therein.

Tamiasciurus in the Black Hills seems to utilize cavities of trees more frequently than outside nests, especially when rearing young. On 27 June 1967, a male was shot from a den tree in Vanocker Canyon, Meade County. The hollow pine tree was 30 feet in height and about 1.5 feet in diameter; the nest entrance was 2.5 inches in diameter and located near the top of the tree. After the den tree was pushed over, it was split open for a better view of the nest. Within the hollow was not one, but a sequential series of nests, graduated in age from bottom to top, comprising about 10 linear feet of nesting material—fine dried grasses and "old-man's beard" (*Chionanthus virginicus*). The series of nests indicates usage of the tree cavity by one or more squirrels over a long period of time. Another nest was extracted from a hollow tree northeast of Custer on 24 June 1967; approximately 538 cubic inches of

dried grasses and finely shredded bark constituted the nest material.

Foods of red squirrels in the Hills consist mainly of seeds of coniferous trees, but bracket fungi and acorns of bur oak also are consumed. A conifer cone is stripped of all its scales as the squirrels eat the ovules, dropping the gnawed core to the ground. These cuttings generally accumulate beneath den or nest trees, forming large middens (accumulations of refuse about a dwelling place). Some middens that I have examined were several feet in depth and exceeded 10 feet in diameter. Bailey (1888:436) noted that red squirrels abide in rocky bluffs and store cones in clefts among the rocks; he also reported extracting two or three bushels of cones from a hollow pine that contained a nest. In addition to cone scales and cores, pine and spruce needles, gnawed twigs and bones, and other litter of food-remains comprise the bulk of such middens. A maze of underground burrows and blindly-ending pockets quite often penetrate these deposits. In the northern Hills, cores of white spruce cones are more predominant in refuse piles than are those of ponderosa pine. Frequently, abandoned barns or feed-bins, and attics of deserted buildings are sites of vast middens and food caches.

Vernon Bailey obtained two lactating adult females southwest of Custer on 26 May 1894, and Ned Dearborn captured another at Redfern on 30 May 1910. Five of 16 females collected in June were nursing, and the uteri of three others evidenced 4 (3-5) placental scars; four additional adult females showed no signs of reproductive activity. Four pregnant red squirrels (the only ones encountered in this study) taken between 20 and 28 June carried 5 (4-6) embryos that were 21.5 (6-42) in crown-rump length. The average length of testes of 17 adult males captured in the period 1 to 15 June was 14.2 (8-22), whereas that of 18 males taken between 16 and 30 June was 17.3 (8-31). Fifteen of 26 females obtained in July were lactating and 11 were reproductively inactive; the average testicular length of 18 July-taken adult males was 16.6 (5-25).

Utilizing the aging criteria of Layne (1954:251), 47 juvenile and subadult *T. hudsonicus* taken (between 10 June and 15 August) in the Hills were grouped into age classes. Time of capture was then projected backward to estimate time of birth of these individuals; 10.6 percent were born in late March, 29.8 percent in early April, 44.7 percent in late April, and 14.9 percent in early May. The occurrence of pregnant females in late June (coincident with attainment of maximal summer testicular length in males) intimates that some adult females in the Black Hills produce two litters, one in spring and the other in midsummer, or else that some females breed later.

Layne (1954:232-235) described the seasonal change in pelage of *Tamiasciurus hudsonicus loquax* in central New York; in general, my observations of molt in *dakotensis,* although somewhat less detailed, concur with his. Adults replace body pelage twice each year. Progress of molt is gradual and somewhat diffuse, usually lacking distinct lines. Adults collected in late May, throughout June, and in early July were in various stages of pelage replacement. Several lactating females still retained irregular patches of winter pelage on the rump in late June and early July. Two adult males captured at Sundance on 18 August 1913 were in full summer pelage, as were six individuals obtained in October. An adult male obtained at Jewel Cave National Monument on 20 November 1967 was in process of autumnal molt; new hairs were manifest beneath the older pelage over the shoulders, sides and venter. Layne (*loc. cit.*) noted that hairs on the tail of adults are replaced but once annually, during the fall molt.

Young red squirrels obtained in June generally were in fine soft juvenal pelage, whereas seven young captured in mid-July were in fresh subadult pelage (similar to adult summer pelage) and two

others were undergoing pelage replacement over most of the body.

A male taken 2 mi W Nemo on 2 July 1967 was parasitized externally by ticks, *Dermacentor andersoni* Stiles, and another male from southwest of Sturgis harbored chiggers, *Miyatrombicula esoensis* (Susa and Ogota). In addition, red squirrels throughout the Black Hills were infested with unidentified fleas (unfortunately, collected specimens of these ectoparasites were misplaced).

Comparison of 24 male and 31 female *T. hudsonicus* from the Black Hills revealed no secondary sexual dimorphism in coloration or external and cranial measurements. Eight squirrels (four males and four females) from north of Sundance are somewhat paler (27.4± 2.68), and reflect reds (54.6±0.15) more intensely and greens (25.3±0.10) less intensely than typical Black Hills representatives; conversely, seven individuals (three males and four females) from south of Tinton are comparatively dark (25.6±1.75), and reflect reds (51.7± 0.17) less intensely and greens (26.5± 0.08) more intensely than do other Hills squirrels.

Tamiasciurus hudsonicus dakotensis differs from *T. h. baileyi*, which occurs west of the Black Hills, in being larger in most external and cranial dimensions, and more reddish in color (reflecting red hues more intensely, Tables 12 and 13). It differs from *T. h. fremonti*, to the south-

TABLE 12.—Geographic variation in coloration of the mid-dorsal pelage of adult *Tamiasciurus hudsonicus* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
55 (24♂, 31♀)	*T. h. dakotensis*, Black Hills, South Dakota and Wyoming			
Mean	26.0	53.3	25.8	20.9
SD	±2.19	±0.16	±0.10	±0.13
6 (2♂, 4♀)	*T. h. dakoteusis*, Converse County, Wyoming			
Mean	30.7	53.9	25.3	20.8
SD	±2.77	±0.18	±0.13	±0.08
7 (3♂, 4♀)	*T. h. dakoteusis*, Carter County, Montana			
Mean	20.6	51.5	26.7	21.8
SD	±3.36	±0.36	±0.19	±0.22
27 (16♂, 11♀)	*T. h. baileyi*, Johnson and Big Horn counties, Wyoming			
Mean	22.3	50.1	27.2	22.7
SD	±1.92	±0.15	±0.09	±0.12
4 (2♂, 2♀)	*T. h. baileyi*, southeastern Albany County, Wyoming			
Mean	27.6	49.3	27.2	23.5
SD	±3.35	±0.14	±0.07	±0.12
10 (4♂, 6♀)	*T. h. baileyi*, Fergus County, Montana			
Mean	25.1	49.4	26.9	23.7
SD	±2.32	±0.19	±0.13	±0.14
10 (6♂, 4♀)	*T. h. fremonti*, Carbon and southwestern Albany counties, Wyoming			
Mean	23.0	48.3	27.8	23.9
SD	±1.45	±0.14	±0.14	±0.97

TABLE 13.—Geographic variation in selected external and cranial measurements of adult *Tamiasciurus hudsonicus* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Ear length	Weight	Greatest length of skull	Rostral length	Zygomatic breadth	Postorbital constriction	Length of maxillary tooth-row
55 (24♂, 31♀)	*T. h. dakotensis,* Black Hills, South Dakota and Wyoming							
Mean	347.7	27.4	291.9	50.3	19.0	29.1	14.3	9.0
SD	±18.40	±2.34	±27.70	±0.89	±0.52	±0.83	±0.44	±0.31
6 (2♂, 4♀)	*T. h. dakotensis,* Converse County, Wyoming							
Mean	343.5	26.0	250.3	48.6	18.8	28.4	14.5	8.0
SD	±17.24	±0.89	±15.71	±0.73	±0.56	±0.26	±0.64	±0.37
7 (3♂, 4♀)	*T. h. dakotensis,* Carter County, Montana							
Mean	340.9	27.4	289.4	49.9	19.3	29.0	14.3	9.0
SD	±13.91	±1.15	±18.09	±1.23	±0.49	±0.86	±0.35	±0.27
27 (16♂, 11♀)	*T. h. baileyi,* Johnson and Big Horn counties, Wyoming							
Mean	328.9	25.8	245.4	49.0	18.4	28.1	14.6	8.7
SD	±20.92	±1.80	±39.24	±0.93	±0.53	±0.93	±0.42	±0.29
4 (2♂, 2♀)	*T. h. baileyi,* southeastern Albany County, Wyoming							
Mean	338.0	23.7	238.5	49.3	19.3	29.2	15.2	8.5
SD	±14.44	±5.91	±36.01	±0.40	±0.50	±0.43	±0.63	±0.13
10 (4♂, 6♀)	*T. h. baileyi,* Fergus County, Montana							
Mean	342.8	25.4	284.3	49.0	18.5	28.6	14.5	8.6
SD	±8.01	±2.46	±44.34	±1.50	±0.59	±0.73	±0.21	±0.20
10 (6♂, 4♀)	*T. h. fremonti,* Carbon and southwestern Albany counties, Wyoming							
Mean	327.8	26.2	240.5	48.7	19.4	28.5	15.1	8.4
SD	±12.72	±2.39	±18.06	±0.57	±0.47	±0.67	±0.53	±0.24

west, in the same manner but to a greater extent. Specimens of *fremonti* reflect greens and blues much more intensely than do those of *dakotensis*. When tone and hue are analyzed separately (see methods and materials), red squirrels are found to vary considerably in tone of color, but the three races discussed here do not differ significantly in this parameter; rather, the races are differentiated on basis of reflection of the various hues.

Because subspecific identification of red squirrels from several areas in southeastern Montana and Wyoming is open to question (Hoffmann and Jones, 1970: 374, Fig. 7), these outlying populations also were examined (Tables 12 and 13). Specimens taken 21.5 mi S, 24.5 mi W Douglas, Converse Co., Wyoming, represent intergrades between *baileyi* and *dakotensis*, but on basis of color are assigned here to the latter. Individuals from a little farther south (southeastern Albany County), however, are clearly *baileyi*. Red squirrels from Carter County, Montana, also are here designated as *dakotensis* on the basis of size and color.

Layne (1954:230) observed the frequency in occurrence of the minute first upper premolar of *T. h. loquax* to be 67.7 percent in males and 70.3 percent in females, and indicated that Bangs (1896) noted this tiny tooth was absent in more than 50 percent of *T. h. hudsonicus* examined. (In consulting the literature, I find no such statement by Bangs.) A peg-like first premolar was visible in the skulls of 18 percent of 55 adult males and in 25 percent of 40 adult females of *dakotensis* examined from the Black Hills. Measurements additional to those

in Table 13 of 55 Hills specimens are: tail length, 137.6±9.44; hind foot length, 52.0±4.00; and skull depth, 21.8±0.80.

Specimens examined (295).—SOUTH DAKOTA: *Lawrence County:* Spearfish, 6 (5 SDSU, 1 USNM); Big Spearfish Canyon, 3 mi S Spearfish, 4200 ft, 1; Big Spearfish Canyon, 5 mi S, 2 mi E Spearfish, 4800 ft, 1; Whitewood, 4 (USD); Tinton, 2 mi N, 13 mi W Lead, 6000 ft, 4; 2 mi S Tinton, 6100 ft, 22; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 6; Little Spearfish Canyon, Savoy, 1 (USNM); Annie Creek, 6500 ft, 1 (USNM); 8 mi W Lead, 2 (SDSU); Deadwood, 6 (USNM); 4 mi SW Lead, 1 (NRW); Terry Peak, 1 (NRW); 1 mi S, 7 mi W Lake Roubaix, 1; 4 mi N, 1 mi W Nemo, 4900 ft, 1; 2 mi W Nemo, 4700 ft, 10; 1 mi E Nemo, 4700 ft, 1. *Meade County:* Vanocker Canyon, 4 mi S, 1 mi W Sturgis, 4600 ft, 1; Haven Dams, 6 mi S, 1.5 mi W Sturgis, 4600 ft, 8; 9 mi S, 1 mi W Sturgis, 4800 ft, 3. *Pennington County:* Rochford, 6 (UMMZ); 6 mi N, 2 mi W Silver City, 1; Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 17; Beaver Creek, 3 mi N, 9 mi W Deerfield, 6500 ft, 2; 5 mi S, 1 mi W Pactola Lake, 1 (SDSU); Pactola Dam, 1 (SDSU); 10 mi W Rapid City, 1 (SDSU); South Canyon, 4 mi W Rapid City, 6 (AMNH); Rapid City, 1 (SDSU); Dark Canyon, 2 mi S, 4 mi W Rapid City, 3 (AMNH); Deerfield Lake, 6400 ft, 2; Deerfield, 1 (SDSU); Redfern, 2 (USNM); 5 mi S, 1 mi W Pactola Lake, 1 (SDSU); 1 mi W Rockerville, 1 (NRW); Spring Creek, south of Rapid City, 2 (MHM); Ditch Creek, 14 mi W Hill City, 6400 ft, 37; Glendale, 8 (7 AMNH, 1 FMNH); Hill City, 3 (USNM); 2 mi SW Medicine Mountain, 1 (SDSU); 3-4 mi SE Hill City, 5300-5400 ft, 16 (UMMZ); Summit Peak, 5500 ft, 1 (UMMZ); Horsethief Lake, 3 mi W Mount Rushmore, 5100 ft, 1; near Mount Rushmore, 1 (UMMZ); 1 mi S Keystone, 1 (NRW); 20 mi N Elk Mountain, 6000 ft, 1 (USNM); 17 mi NW Custer, 2 (UMMZ); 16 mi NW Custer, 3 (UMMZ); unspecified locality, 4 (1 SDSU, 3 UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 2 (FMNH); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 7; 5.75 mi N, 5.75 mi E Custer, 5220 ft, 8; Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 6; 4 mi N, 14 mi W Custer, 2; 4 mi N, 4.5 mi E Custer, 5400 ft, 1; Tepee Canyon, 14 mi W Custer, 3 (USNM); Custer, 7 (1 SDSU, 6 USNM); Harvey National Forest, 3 mi E Custer, 2 (UMMZ); Custer State Park, 5 (UMMZ); Squaw [=Grace Coolidge] Creek, 5 (3 AMNH, 2 FMNH); Jewel Cave National Monument, 2.5 mi S, 12 mi W Custer, 5400 ft, 1; 7 mi SW Custer, 1 (SDSU); Elk Mountain, 1 (USNM), unspecified locality, 1 (UMMZ). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 1. *Unspecified county:* Black Hills, 3 (1 NRW, 1 SDSU, 1 USNM).

WYOMING: *Crook County:* Devils Tower, 4 (USNM); 15 mi N Sundance, 5500 ft, 1; 15 mi ENE Sundance, 3825 ft, 7; 3 mi NW Sundance, 5900 ft, 16; Sundance, 2 (USNM); unspecified locality, 1 (SDSU).

Additional records.—SOUTH DAKOTA: *Lawrence County:* Lead (Chambers, 1948:8). *Custer County:* 16 mi SW Custer (USBS files). WYOMING: *Weston County:* head Cheyenne River (J. A. Allen, 1877:689).

Glaucomys sabrinus bangsi (Rhoads)

Northern Flying Squirrel

Sciuropterus alpinus bangsi Rhoads, 1897, Proc. Acad. Nat. Sci. Philadelphia, 49:321, 19 July (type locality, Raymond, Bear Lake Co., Idaho).

Glaucomys sabrinus bangsi—A. H. Howell, 1918, N. Amer. Fauna, 44:38, 13 June.

Glaucomys sabrinus occurs in montane habitats of the western United States, and in boreal forest areas of northern North America. In the Black Hills, this squirrel is most abundant in the spruce forests of moist canyon systems on the boreal cap, but ranges down to about 4500 feet. Specimens are lacking for Meade, Custer, and Fall River counties; however, residents report that this species is a common mammal throughout the study area, and is active the year around. Grinnell (1875:81) first noted flying squirrels in the Hills, under the name *Pteromys alpinus.*

Northern flying squirrels are somewhat gregarious in the colder months. J. A. King captured 10 individuals in a spruce-filled canyon southeast of Hill City between 11 December and 29 March; three of these were obtained from the same tree. These specimens were taken in rat traps that were attached to trees about seven feet above ground level and baited with peanuts. South of Tinton, remains of a flying squirrel were found in the center of a midden of pine cones at the base of a dead tree.

Most of the recently collected specimens have been obtained by tapping on dead hollow trees and shooting the squir-

rels as they exited from the den. Trees selected as nest sites usually are high on slopes wooded in pine and scattered spruce and aspen. The average height of five nest trees was 18.6 (15 to 25) feet, and all were about one and a half feet in diameter; openings to these nests were 12.8 (10 to 18) feet above ground surface. The oval-shaped entrance to one nest was 57 by 67 millimeters in diameter; depth and width of the nest cavity were 145 and 100 millimeters, respectively; the spherical nest was composed of fine grass and "old-man's beard." Flying squirrels were obtained from nests east of Buckhorn, Wyoming, on 18 July 1951 (one lactating adult female and four juveniles, of which two were males and two were females), and west of Nemo, South Dakota, on 29 June 1967 (one lactating adult female and two juveniles, one male and one female), on 4 July 1967 (one adult male), and on 5 July 1967 (one lactating adult female and three juveniles, of which two were males and one was a female).

Reproductive data essentially are lacking for this species in the Black Hills except for the nest-taken individuals mentioned above. Testes of an adult male taken on 4 July were 11 in length. Young flying squirrels are in evidence through August. These have a fine short juvenal pelage that generally is darker than that of adults; the tail is blackish rather than cinnamon. *Glaucomys sabrinus* from the Black Hills were parasitized externally by an unidentified flea.

A. H. Howell (1918:38) referred two specimens of *G. sabrinus* from the Bear Lodge Mountains to the subspecies *canescens,* indicating that these individuals approached *bangsi* in skull characters and in a slightly more vinaceous coloring on the upperparts. When additional specimens were made available through his own field work, King (1951: 469) noted that representatives of *Glaucomys* from the Black Hills differed significantly from *canescens* of North Dakota, but closely resembled three specimens of *bangsi* from Park and Fremont counties, in Wyoming; Long (1965:599) later concurred with King's assignment of flying squirrels in the Black Hills to *G. s. bangsi.*

Neither secondary sexual characteristics nor age groups of adults (age was determined in the manner of King, *loc. cit.*) evidenced significant variation. Individuals from the Hills were compared with specimens from Park, Teton, and Sublette counties, in western Wyoming. Mid-dorsal pelage of animals from the Black Hills is slightly darker in tone, and reflects reds more intensely and greens less intensely than those from western Wyoming; however, these differences are nonsignificant. Means and standard deviations of these color parameters are given for six adults (two males and four females) from the Hills, followed by those for nine adults (four males and five females) from the western Wyoming: color tone, 39.1±2.94, 39.5±4.78; percent red reflectance, 51.2±0.12, 50.0±0.28; percent green reflectance, 26.1±0.07, 27.3±0.16; percent blue reflectance, 22.7±0.08, 22.7±0.16.

External and cranial dimensions of representatives from the Hills examined in the present study agree closely with those of 12 adults measured by King (*loc. cit.*). However, specimens from the study area are significantly smaller than those from western Wyoming in total length, tail length, ear length, greatest length of skull, and zygomatic breadth. Means and standard deviations of six adults (two males and four females) from the Hills, followed by those of nine adults (four males and five females) from western Wyoming, are: total length, 300.8±11.43, 329.4±9.69; tail length, 133.7±5.28, 150.0±4.08; hind foot length, 40.0±3.35, 41.3±1.11; ear length, 23.3±4.27, 27.3±1.11; weight, 149.8±23.48, 167.5±33.78; greatest length of skull, 40.4±0.69, 41.6±0.81; zygomatic breadth, 24.3±0.25, 25.2±0.50; braincase breadth, 19.3±0.33, 19.5±0.22; postorbital breadth, 9.0±0.39, 9.0±0.50; interorbital breadth, 7.7±

0.30, 8.0±0.63; rostral length, 13.5± 0.32, 13.9±0.59; length of maxillary tooth-row, 8.1±0.14, 8.1±0.35; cranial depth, 17.6±0.51, 18.1±0.55; ratio of cranial depth to breadth of braincase, 0.92 (range: 0.91-0.95), 0.93 (range: 0.89-0.96).

The smaller size, slightly different coloration, and isolation of *G. sabrinus* in the Black Hills (about 245 miles west of populations in Park County, Wyoming) warrant further investigation before an accurate assignment to a subspecies can be made. For the present time, I tentatively retain the subspecific name *bangsi* for the flying squirrels in the Black Hills.

Specimens examined (31).—SOUTH DAKOTA: *Lawrence County:* Little Spearfish Canyon, Timon Campground, 1 (USNM); 2 mi S Tinton, 6100 ft, 1; 2 mi W Nemo, 4700 ft, 7. *Pennington County:* 1 mi N Sheridan Lake, 1 (USNM); Castle Creek, 6500 ft, 2 (UMMZ); 4 mi SE Hill City, 53-5400 ft, 16 (UMMZ); T. 1 N, R. 6 E, sec. 8, 1; 17 mi NW Custer, 1 (UMMZ); 16 mi NW Custer, 2 (UMMZ).

WYOMING: *Weston County:* 0.5 mi N, 3 mi E Buckhorn, 6200 ft, 5.

Additional records.—WYOMING: *Crook County:* middle fork Hay Creek, Bear Lodge Mountains (A. H. Howell, 1918:38).

Family GEOMYIDAE—Pocket Gophers

This family of fossorial rodents has undergone its entire evolutionary history in North and Central America. Pocket gophers, so named because of the fur-lined cheek pouches that open externally on either side of the mouth, are represented by but one species in the Black Hills; a second species (*Geomys bursarius*) has been reported erroneously from the area. Food habits of pocket gophers and their extensive subterranean burrow systems, usually marked by mounds of earth near each entrance, present some economic problems to agricultural and livestock interests; thus control methods such as extensive trapping or poisoning programs have been carried out by ranchers in the Hills region.

Thomomys talpoides nebulosus V. Bailey

Northern Pocket Gopher

Thomomys talpoides nebulosus V. Bailey, 1914, Proc. Biol. Soc. Washington, 27:116, 10 July (type locality, Jack Boyden's Ranch, Sand Creek Canyon, 15 mi NE Sundance, 3750 ft, Crook Co., Wyoming).

The northern pocket gopher is widespread in the Black Hills and common where local environmental factors are favorable. The species inhabits montane meadows and parklands, disturbed areas of secondary vegetative growth, and croplands, but is most abundant in heavily grazed valley pastureland. Specimens are available from throughout the Hills save from Fall River County, but the earthen mounds characteristic of gophers evidence their presence there. Based on specimens at hand, the altitudinal range of *T. t. nebulosus,* a subspecies endemic to the Black Hills, extends from 3500 to 6500 feet. Among 146 individuals examined of which the sex was known, only 41 are males, suggesting that females may be more readily captured in traps. *Thomomys talpoides* was first reported from the Hills by Bailey (1888:450).

The holotype, four allotypes, and specimens from Sundance were taken by Vernon Bailey late in August 1913 in potato fields. Those obtained northeast of Beulah, Wyoming, early in July 1947 were captured in fields of alfalfa. Specimens from Palmer Gulch were trapped in winter in a valley hayfield, between a pine forest and a small stream. Four females were taken in August 1934 in a montane meadow on Doran's Ranch, 3 mi E Custer by Stebler (1939:390) where prominent plants were the short grasses, but clumps of sagebrush, goldenrod, butter and eggs, and asters were conspicuous.

Fifteen individuals from Nemo (late June and early July 1967) were trapped in a grazed pasture of bluegrass, clover, and scattered forbs. Three of eight gophers trapped east of Four Corners early in July 1965 were taken in a burned area on a high ridge on which secondary regeneration of ponderosa pine and many

kinds of forbs had occurred; the others were captured in a pasture of bluegrass and clover. No specimens have been obtained in heavily forested areas.

In early July 1965, a member of a field party from the Museum of Natural History, H. H. Genoways, studied burrow systems of *T. t. nebulosus* and their distribution in Beaver Creek Valley, Pennington County. Mounds were located in dense, sodlike grasses where the soil was extremely dark, moist, and fairly free of rocks, as well as in areas of dry rocky soils that contained much organic material. Burrows generally were located at the edge of mounds. The following average measurements (in millimeters) are of 16 tunnel systems in valley soils: depth from opening of mound to bottom of tunnel, 170 (110-250); width of tunnel, 65 (50-80); and height of mound above ground level, 75 (60-90). Burrows located in rocky soils generally were much shallower, and systems excavated by subadults were at most 80 millimeters below ground level and were situated in relatively deep black soils.

This species often is active in the early afternoon. A female was obtained in Weston County on 7 July 1965 at 15:00 hrs (MDT), shortly after traps were set, and I captured two juveniles about 16:00 hrs (MDT) in snap-traps that were set in a montane meadow southwest of Spearfish on 7 August 1967. Although most of the specimens examined were taken in the summer months, J. A. King obtained individuals from November 1945 through April 1946 in Pennington County. Mounds and tunnel systems formed under the snow usually are evident in spring, a further indication that the northern pocket gopher is active the year around in the Hills.

Testicular length of an adult male captured on 4 July 1967 was 12. Only two pregnant females were observed, one taken on 3 July 1967 at Nemo, South Dakota, and the other collected on 4 July 1965, near Four Corners, Wyoming; each carried four embryos that were 9 and 12 in crown-rump length, respectively. Enlarged uteri, possibly indicating recent implantation were noted in three females obtained in early July 1965 in Beaver Creek Valley; two others were lactating. Placental scars (7, 3, and 3) were evident in three females taken in Lawrence County in 1967 on 29 June, 3 July, and 29 July, respectively. Females probably breed once annually (from mid-March through mid-June) and produce three or four young; thus, the occurrence of seven placental scars in late June is of interest. Placental scars in pocket gophers generally remain two months after parturition (Tryon, 1947:18) but the number of live-born young may be smaller than the embryo count; additional scars probably indicate resorption of some embryos rather than production of two litters at this early date. Hansen (1960:331) reported resorption of about four percent of all embryos examined in a study of *T. talpoides* in Colorado.

Young of the year were captured first in mid-June in the Black Hills and are fairly common in collections made in July; for example, 10 of 15 individuals obtained at Nemo from 29 June to 4 July 1967 are juveniles, as are five of six specimens taken at Beulah on 2 July 1947. Subadults attain about three-quarters of adult size by late July and early August, although younger individuals are still taken occasionally. Two traps placed in the same burrow system at Nemo took an adult female and a juvenile female on 3 July 1967.

Bailey (1915:18) described the process of molt in *T. talpoides*. Progress of the crescentic shaped molt wave is from the rostrum, toward the rump. Young taken in late June and early July were in a fine, juvenal pelage; many subadults trapped late in July were in post-juvenal molt. Two simultaneous molt lines were of common occurrence on spring-taken adult specimens, and five individuals evidence three successive molt lines in progress. Long winter pelage remain on the rump of most specimens until mid-July. A female taken by Merritt Cary

on Elk Mountain, on 19 November 1901 was undergoing molt to winter pelage, whereas three others obtained there about this time were in fresh winter pelage. Four specimens from the Black Hills have patches of white hair on the shoulder or dorsum, and a female from Nemo has a white star-shaped area on the forehead.

A female from Pennington County (2 July 1965) was parasitized externally by two kinds of lice, *Geomydoecus thomomyus* (McGregor), and a new species currently being described by R. D. Price and associates, University of Minnesota.

Analysis of nongeographic variation in northern pocket gophers in the Black Hills revealed no secondary sexual dimorphism in external or cranial dimensions, but tone of color of seven adult males collected in the summer (28.6± 4.38) is significantly paler than that of 20 adult females (23.9±4.30). Because of the topographic diversity in the mountainous terrain, and due to the relatively sedentary nature of pocket gophers, localized populations display great variability in the Hills. For example, individuals from Nemo are darker in tone, reflect blues more intensely, and have greater lengths of skull, rostrum, and maxillary tooth-row than other populations in the Hills.

Thomomys talpoides nebulosus in the Black Hills resembles *T. t. bullatus* of the plains to the west, north and northeast, but is significantly darker in tone and larger in most external and cranial dimensions (see Table 14). Specimens from outlying areas of the Hills (Bear Lodge Mountains, Devils Tower, Four Corners, vicinity of Beulah and near Buckhorn, in Wyoming, and Rapid City, in South Dakota) are paler than typical *nebulosus*, showing a tendency toward *bullatus*, but are best assigned to the former. *Thomomys talpoides nebulosus* differs from *T. t. pierreicolus* of the plains to the east and south in the same manner as described above for *T. t. bullatus*, but to a greater extent. Selected measurements of seven adult males and 24 adult females from the Hills are: percent red reflectance, 45.9±0.24; percent green reflectance, 27.6±0.13; percent blue reflectance, 26.5±0.20; body length, 226.3± 9.34; tail length, 66.6±6.58; hind foot length, 29.1±2.36; ear length, 6.8± 0.88; weight, 140.6±19.78; greatest length of skull, 38.9±1.61; zygomatic breadth, 23.2±0.94; rostral length, 17.1 ±1.09; interorbital constriction, 6.6±

TABLE 14.—Geographic variation in selected color, and external and cranial measurements of adult *Thomomys talpoides* from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Total body length	Tail length	Hind foot length	Weight	Greatest length of skull	Rostral length	Length of maxillary tooth-row	Skull depth
31 (7♂, 24♀)			*T. t. nebulosus*, Black Hills, South Dakota and Wyoming						
Mean	25.1	266.3	66.6	29.1	140.6	38.9	17.1	7.9	15.3
SD	±4.72	±9.34	±6.58	±2.36	±19.78	±1.61	±1.09	±0.39	±0.80
13 (6♂, 7♀)			*T. t. bullatus*, Harding County, South Dakota						
Mean	37.0	213.7	64.5	27.5	130.5	38.0	16.2	7.6	14.5
SD	±6.85	±10.99	±6.13	±1.39	±22.28	±1.85	±0.90	±0.32	±0.49
9 (1♂, 8♀)			*T. t. bullatus*, Campbell County, Wyoming						
Mean	33.2	212.9	60.9	27.9	109.2	37.4	16.2	7.7	14.7
SD	±1.37	±9.20	±4.23	±1.27	±11.34	±0.86	±0.58	±0.32	±0.59
4 (1♂, 3♀)			*T. t. pierreicolus*, Dawes County, Nebraska						
Mean	32.1	199.7	54.2	27.0	92.8	35.5	14.4	7.1	14.3
SD	±3.82	±4.27	±2.63	±1.15	±5.92	±0.96	±0.54	±0.26	±0.46

0.34; length of maxillary tooth-row, 7.9 ±0.39; depth of skull, 15.3±0.80.

Specimens examined (158).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 9 mi S, 3 mi W Spearfish, 5000 ft, 2; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 2; 2 mi S Tinton, 6100 ft, 2; 2 mi N, 4 mi W Nemo, 5100 ft, 3; Nemo, 5700 ft, 15; unspecified locality, 1 (NRW). *Meade County:* Fort Meade, 1 (USNM). *Pennington County:* Rapid City, 2 (USNM); Spring Creek, south of Rapid City, 2 (MHM); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 3; Beaver Creek, 3 mi N, 9 mi W Deerfield, 6500 ft, 3; 20 mi N Elk Mountain, 2 (USNM); Ditch Creek Valley, 14 mi W Hill City, 6400 ft, 1; 2 mi S, 13 mi W Hill City, 1; Palmer Gulch, 3 mi SE Hill City, 5300 ft, 14 (UMMZ); Tigerville, near Hill City, 2 (USNM); Redfern, 4 (USNM); 16 mi NW Custer, 3 (UMMZ); Harney National Forest, 3 mi E Custer, 4 (UMMZ); unspecified locality, 6 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 4 (FMNH); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 1; Bull Springs, 2 mi N, 9 mi W Custer, 6 (UMMZ); Custer, 5 (4 USNM, 1 AMNH); Mayo, 3 (USD); Campbell's Ranch, Elk Mountain, 4800 ft, 1 (USNM); Elk Mountain, 7 (USNM); 1 mi N Wind Cave, Wind Cave National Park, 1 (WCNP); Wind Cave National Park, 1 (USNM); Beaver Creek, 1 (USNM).

WYOMING: *Crook County:* 1 mi E, 0.5 mi N Beulah, 3550 ft, 14; Beulah, 3500 ft, 6; Bear Lodge Mountains, 6200 ft, 6 (USNM); Devils Tower, 1 (USNM); 1.5 mi NW Sundance, 5000 ft, 4; Sundance, 2 (USNM); Rattlesnake Creek, 6000 ft, 2 (USNM); Sand Creek, 5 mi above mouth of canyon, 5 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 2; 4 mi E Four Corners, 8; Newcastle, 5 (USNM).

Additional record.—SOUTH DAKOTA: *Lawrence County:* Deadwood (Bailey, 1888: 450).

Family HETEROMYIDAE—Pocket Mice and Kangaroo Rats

Three species (two genera) of heteromyids are represented in the mammalian fauna of the Black Hills; a fourth species occurs nearby and its status in the Hills region remains uncertain. All members of this family possess external, fur-lined cheek pouches, and to varying degrees are nocturnal, fossorial, and saltatorial. These rodents inhabit the interface of the foothills and surrounding semiarid plains, particularly on fine loamy soils of the Sand Hill Regosol Soil Subassociation along the South Dakota-Wyoming border.

Perognathus fasciatus olivaceogriseus Swenk

Olive-backed Pocket Mouse

Perognathus flavescens olivaceogriseus Swenk, 1940, Missouri Valley Fauna, 3:6, 5 June (type locality, Little Bordeaux Creek, sec. 14, T. 33 N, R. 48 W, 3 mi E Chadron, Dawes Co., Nebraska).

Perognathus fasciatus olivaceogriseus—Jones, 1953, Univ. Kansas Publ., Mus. Nat. Hist., 5:520, 1 August.

The olive-backed pocket mouse inhabits gravelly soils on the high plains peripheral to the Black Hills, and occasionally, individuals are taken in the foothill transition zone. The species has been captured only at four localities within the Hills of which two are in South Dakota, and two are in Wyoming. Altitudinal range as indicated by these specimens is up to 4800 feet.

Most available specimens of this species were obtained in the Hills area in the early part of the present century, but they first were reported from the area by Jones (1953:522): Merritt Cary captured five females in early October 1903 in Custer County; Vernon Bailey obtained a male near Newcastle, on the western border of the Hills, on 24 May 1894, and in August 1913 found a mummified individual of unknown sex near Sundance, Wyoming.

I obtained two specimens while trapping in Wind Cave National Park in 1968; a female was taken on 29 July (partially eaten in the trap by a chipmunk) and a male on 28 August. Both individuals were captured in snap-traps baited with rolled oats and placed in sparse grass at the junction of a fence row and a gravel road; the fence encircled a sewage-settling pond at the head of Wind Cave Canyon. *Microtus ochrogaster, Peromyscus maniculatus, Reithrodontomys megalotis, Perognathus hispidus,* and *Eutamias minimus* were taken in the same trapline.

The female taken in 1968 was neither pregnant nor lactating; reproductive data are unavailable for those females captured by Cary. Testes of the adult male from Wind Cave Canyon were 3 in length.

Specimens examined (8).—SOUTH DAKOTA: *Custer County:* Campbell's Ranch, Elk Mountain, 4800 ft, 5 (USNM); Wind Cave Canyon, Wind Cave National Park, 4100 ft, 1. WYOMING: *Crook County:* Sundance, 1 (USNM). *Weston County:* Newcastle, 1 (USNM).

Perognathus hispidus paradoxus Merriam

Hispid Pocket Mouse

Perognathus paradoxus Merriam, 1889, N. Amer. Fauna, 1:24, 25 October (type locality, Banner, Trego Co., Kansas).

Perognathus hispidus paradoxus—Osgood, 1900, N. Amer. Fauna, 18:44, 20 September.

The hispid pocket mouse ranges across the short and mixed grass prairie of western South Dakota and eastern Wyoming (Glass, 1947:179). Although uncommon, it has been taken in the foothill transition zone of the Black Hills at altitudes up to 4800 feet. Specimens have been obtained only in Custer and Fall River counties.

Three females were captured by Merritt Cary on Campbell's Ranch, Custer County, in the early 1900's, and a field party from The University of Kansas found a male dead along a road 3 mi E Pringle in mid-June 1961. A juvenal female was trapped southwest of Minnekahta in mid-June 1967, along an overgrown fence row that was bordered on both sides by barren agricultural fields. The fence was paralleled by a strip of dense vegetation about 10 feet in width, consisting of Japanese brome, western wheat grass, bluegrass, and a few forbs.

Two males were taken in late summer of 1937 in Wind Cave National Park by E. Suter. I obtained a female in the Park in mid-August 1967 and a male at the head of Wind Cave Canyon in late August 1968. The female was carrying unidentified seeds in her cheek pouches and was trapped along a high fence that separates the National Park from Custer State Park. Vegetation, mainly grasses, on the Wind Cave side of the fence was tall and dense. Due to overgrazing by bison in Custer State Park, vegetation was sparse and short on that side of the fence. The male was trapped in an open habitat of sparse vegetation, where the soil was rocky, being similar to a gravel pavement. *Microtus ochrogaster, Peromyscus maniculatus, Reithrodontomys megalotis, Perognathus fasciatus,* and *Eutamias minimus* were taken in association with *P. h. paradoxus.*

Reproductive data concerning females captured by Cary are unavailable; however, the female collected on 18 August 1967 carried six embryos that each were 15 in crown-rump length, and testes of the adult male taken on 27 August 1968 were 5 in length. The juvenal female (17 June 1967) was in fresh pelage that was fine in comparison to the rather coarse fur of adults. The male from Wind Cave Canyon was parasitized externally by ticks, *Ixodes spinipalpis* Hadwen and Nuttall.

Specimens examined (9).—SOUTH DAKOTA: *Custer County:* Campbell's Ranch, Elk Mountain, 4800 ft, 3 (USNM); 3 mi E Pringle, 1; Wind Cave National Park, 2 (WCNP); 6 mi N, 1 mi E Wind Cave, Wind Cave National Park, 4400 ft, 1; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 1. *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 1.

Dipodomys ordii luteolus (Goldman)

Ord's Kangaroo Rat

Perodipus ordii luteolus Goldman, 1917, Proc. Biol. Soc. Washington, 30:112, 23 May (type locality, Casper, Natrona Co., Wyoming).

Dipodomys ordii luteolus—Grinnell, 1921, Jour. Mamm., 2:96, 2 May.

Ord's kangaroo rat occurs on the plains that surround the Black Hills, and on sandy soils with sparse ground cover and an abundance of seed plants. Occasionally, these rats also range into the foothill transition zone. Merritt Cary collected a male and a female on Campbell's Ranch at Elk Mountain early in

October 1903 and N. R. Whitney obtained a male south of Cascade Springs, Fall River County, on 8 February 1957. Two other individuals were taken along the eastern periphery of the Hills, south of Rapid City, sometime between 1899 and 1911 by Henry Behrens. D. G. Adolphson recently obtained skulls of this species from barn owl pellets collected 15 mi S Hot Springs (Martin, 1971a:4; 1971b).

The female from Elk Mountain, taken on 10 October, evidenced molt on the dorsum; no other life history data are at hand for the specimens examined.

Specimens examined (5).—SOUTH DAKOTA: *Pennington County:* Spring Creek, south of Rapid City, 2 (MHM). *Custer County:* Campbell's Ranch, Elk Mountain, 4800 ft, 2 (USNM). *Fall River County:* south of Cascade Springs, 1 (NRW).

Dipodomys ordii terrosus Hoffmeister

Ord's Kangaroo Rat

Dipodomys ordii terrosus Hoffmeister, 1942, Proc. Biol. Soc. Washington, 55:165, 31 December (type locality, Yellowstone River, 5 mi W Forsyth, 2750 ft, Rosebud Co., Montana).

Habits of this heteromyid are similar to those of the preceding subspecies. Vernon Bailey obtained three males and four females near Newcastle, Wyoming in late May 1894. When he examined kangaroo rats from the Northern Great Plains region, Setzer (1949:524 and 543) designated those specimens from Elk Mountain (in the Black Hills proper) as *D. o. luteolus* and indicated that other individuals from near Newcastle (on the western periphery of the Hills) were intergrades between *D. o. luteolus* and *D. o. terrosus*, but were assignable to the latter. *D. o. terrosus* is discernibly darker and larger than *luteolus* except for a shorter tail and external ear pinna (Long, 1965:618).

Further collecting is requisite along the western border of the Hills to provide critical data concerning the status of these two subspecies in that region. Until further specimens are available, I follow Setzer.

Specimens examined (7).—WYOMING: *Weston County:* Newcastle, 7 (USNM).

Family CASTORIDAE—Beavers

The beaver is the largest rodent in North America. Prior to the appearance of European man in the region, beaver were of great abundance and played a major role in luring early adventurers to the Black Hills. For example, expeditions of the Verendrye brothers in 1743, the American Fur Company in 1811, Jedediah Smith in 1823, and untold number of traders, trappers, and mountain men in the early 1800's mainly were in search of beaver and the premium prices paid for beaver pelts at that time.

Morgan (1868:137) indicated that beavers migrate each year, particularly when an area becomes overstocked. He noted that an annual migration down the Missouri River usually occurred in June, and wrote as follows: "A trapper whom I met on the Missouri River in 1862, below Fort Pierre, in Nebraska [present day South Dakota], informed me that beavers were then (May 27) coming down the river; that he saw them daily and had taken over fifty." Incidentally, Morgan (1868:209) gave a description of the natural vegetation along the Missouri River as it appeared in the 1860's, before modification by white man.

As evidenced by numerous houses and dams along most streams, beaver were abundant in the Black Hills at the time of the Custer Expedition in 1874 (Grinnell, 1875:82; Ludlow, 1875:15; O'Hara, 1929:252) and the Newton-Jenney Expedition in 1875 (Dodge, 1876:123). Increased colonization caused reductions in numbers of beavers, and Bailey (1888:441) reported that in the autumn of 1887, only a few were "still found in places far back from settlements" in the Black Hills region. Inadequate game protection laws were ineffectively enforced by the state of South Dakota between 1871 and 1889 (Elley, 1945:5), and intensive trapping steadily reduced population levels. According to Harris and Aldous (1946:348), the spe-

cies was nearly extinct in western South Dakota by 1927, but, reports of Seton (1929c:453) and District Forester Allen S. Peck (U. S. Biological Survey files) indicated that more than two thousand beaver inhabited the Black Hills National Forest at this time. In 1927, a nonpolitical form of Game Commission was established (Elley, *loc. cit.*), and responsible management practices were initiated by the South Dakota Department of Fishes, Game and Parks in the 1930's. Beaver were restocked in the Hills from populated streams elsewhere in South Dakota. For example, due to the surplus of beaver along the James, Vermillion, and Sioux rivers in the southeastern part of the state in 1940, 300 of these large rodents were transplanted to the Hills (Wildlife Tips and Briefs, 1:14-15, 8 November 1940). Sale of 1196 beaver pelts netted trappers in the Black Hills $35,285.00 in 1945 (Elley, *loc. cit.*). Adequate protection, in conjunction with the relatively low prices now being paid for beaver pelts, have allowed the species to increase in the Hills to the point that it now is overusing the habitat. In recent years, beaver have caused extensive damage to white birch, aspen, poplar, willow, and cottonwood trees along many drainage systems (South Dakota Conservation Digest, 24:12, October, 1957).

Dams of this aquatic mammal regulate runoff by impounding water, thus aiding in the control of erosion and the maintenance of an adequate water table. Sediment gradually accumulates behind the dams and many former beaver ponds eventually are transformed into meadows, thereby increasing the stock carrying capacity of the range. Berner (1953b:9) noted that the three to four thousand beaver in the Black Hills National Forest, in combination with the grazing activities of cattle, have been, and still are, converting many brushy bottomlands into bluegrass pastureland.

Castor canadensis missouriensis Bailey

BEAVER

Castor canadensis missouriensis Bailey, 1919, Jour. Mamm., 1:32, 28 November (type locality, Apple Creek, 7 mi E Bismarck, Burleigh Co., North Dakota).

The beaver is found on every major creek and river in South Dakota, but it is most numerous in the Black Hills where hundreds of beaver dams decorate the countryside (Gilliland, 1968b:5). Morgan (1968:130) first reported this species from the study area when he observed that the numerous dams on streams of the Black Hills were unusually small (in comparison to those he studied around Lake Superior), ranging from 50 to 100 feet in length and two to three feet in height.

Castor canadensis missouriensis differs from *C. c. concisor* of south-central Wyoming in its slightly paler underparts, relatively broader zygomata, more open orbit, narrower nasals, and in the shape of the jugal (Long, 1965:622-623).

Some stocks of beaver have been introduced into the Black Hills from areas outside of South Dakota. For instance, three young from Yellowstone National Park were planted along Squaw [=Grace Coolidge] Creek in Custer State Park in 1914, and another family of beaver was added in 1916 (South Dakota Conservation Digest, 36:3, 1969). Sixty beaver were transplanted to the Hills from an unmentioned source in 1932; a pair on Jim Creek and another pair along Cold Springs Creek produced five and three young, respectively (reports of Regional Ranger, Black Hills National Forest, U. S. Biological Survey files). In 1947, five white beaver were observed along Grizzly Creek, a pair of which was captured and placed in the Custer State Park Zoo (American Fur Breeders, 21:62, December, 1948; Game News of Pennsylvania, 19:16, March, 1949).

From 1936 to 1944, 34 artificial sites, consisting of small dams and temporary bank lodges, were constructed in the northern Black Hills (Harris and Aldous, 1946:349). One hundred and thirty-six beaver were released at these artificial sites and 259 were released at natural sites. Members of the latter group tended to move on to other areas, whereas beaver became established on 31 of the

artificial sites. Of 100 beavers tagged and released in the period 1942 to 1944, 14 were retaken (*op. cit.*:350); time between release and recapture averaged 11.9 (1 to 33) months. One individual was obtained at the site of release; and the remaining 13 individuals moved an average of 9.1 (3 to 30) miles before being recaptured. The average rate of movement was 3.2 (0.3 to 14.0) miles per month. In all, 1892 beaver were trapped in 700 square miles of the northern Black Hills from 1936 to 1945; in a five-day period in November 1944, 25 beaver were captured near the head of the South Fork of Boxelder Creek (*loc. cit.*).

Gilliland (1968b:5) noted that colonies in the Black Hills consist of one or more families (one to 12 beavers) of all age groups (i. e., parents, kits, and yearlings). Two to eight kits usually are born between late April and early June.

Specimens examined (5).—SOUTH DAKOTA: *Lawrence County:* Tinton, 2 mi N, 13 mi W Lead, 6000 ft, 1; 2 mi S Tinton, 6100 ft 1. *Pennington County:* Rapid Creek, 1.5 mi W Rochford, 5300 ft, 1 (UMMZ); Spring Creek, south of Rapid City, 1 (MHM). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 1 (FMNH).

Family CRICETIDAE—Native Rats, Mice, and Voles

This family includes a large assemblage of terrestrial or partially fossorial rodents representing two subfamilies in the Black Hills. The more primitive cricetines are nocturnal in habit and are characterized by cheekteeth that bear two longitudinal rows of tubercles. The genus *Neotoma* is an exception; its teeth are cuspless, being formed instead of occlusal lakes of dentine surrounded by enamel. The more advanced microtines may be active for short periods throughout any given 24-hour period, usually following well established runways, and are characterized by rootless, prismatic cheekteeth that lack enamel on occlusal surfaces.

Three cricetine genera (four species) and three microtine genera (five species) in habit the Black Hills. The status of three additional cricetids (two cricetines and one microtine) in the Hills region remains uncertain, and another microtine has been incorrectly reported from the area.

As part of their reforestation program, the U. S. National Forest Service maintains numerous ponderosa pine plantations throughout the Black Hills. These sites are prepared by windrowing, and the resulting dense grass and forb composition that develops in these windrows provides excellent habitat for small mammals. Periodically, populations of microtines in these areas increase to levels that are not controlled by predators and tremendous damage to pine plantings results. Such a population buildup of voles occurred in winter of 1968-1969, when an 870-acre area in the Bearlodge District suffered 75 percent pine seedling mortality (Fred Wild, Range Conservationist, pers. com.) and the Taylor Divide-Blacktail Creek plantation in the same district was nearly a total loss (John C. Windsor, District Ranger, pers. com.).

Most damage occurred under the cover of snow; bark was removed from the root collar upward to the extent of the protective snow cover. Pine seedlings up to one inch in diameter frequently were gnawed completely through and other species such as aspen and oak were killed by girdling. Subsequent surveys of damaged areas yielded from two to 42 mice per 100 trap nights. For example, on the Dry Beaver Plantations, Pennington County, 20 *Microtus pennsylvanicus*, two *Clethrionomys gapperi* and two *Sorex cinereus* were obtained in 50 trap nights (Fred Wild, pers. com.). The Forest Service plans to attempt control measures on all areas sampled that yielded 15 or more rodents per 100 trap nights (John C. Windsor, pers. com.).

Reithrodontomys megalotis dychei J. A. Allen

Western Harvest Mouse

Reithrodontomys dychei J. A. Allen, 1895, Bull. Amer. Mus. Nat. Hist., 7:120, 21 May (type locality, Lawrence, Douglas Co., Kansas).

Reithrodontomys megalotis dychei—A. H. Howell, 1914, N. Amer. Fauna, 36:30, 5 June.

Reithrodontomys megalotis dychei is distributed throughout the Great Plains of central United States, inhabiting grassy environs, weedy borders of cultivated tracts, thickets of shrubbery, and riparian communities. This mouse is active the year around, and in the Black Hills occurs at elevations up to 6200 feet, although it is most abundant in the transition zone below 5400 feet. The first specimens of the western harvest mouse taken in the study area were obtained by B. Bailey at Spearfish early in August 1927, but *R. megalotis* was not reported from the Hills until much later, by Jones and Mursaloglu (1961:25).

This species is fairly common along the prairie border and through the foothills of the region. Nine individuals from southwest of Minnekahta were trapped in mid-June 1967 along fencerows of bluegrass, brome grass, cord grass, western wheat grass, and scattered forbs, and often were taken in runways of *Microtus ochrogaster*. The mixed-grass prairie lowlands that are interspersed with bushes and young trees in Wind Cave National Park also are inhabited, although to a lesser extent, by harvest mice in association with *Eutamias minimus*, *Perognathus fasciatus*, *P. hispidus*, *Peromyscus maniculatus*, *M. ochrogaster*, and *Mus musculus*. In the Red Valley and foothills, moist draws and riparian communities that support growths of chokecherry, wild plum, wild rose, hackberry, and other thickets of shrubbery provide adequate cover for harvest mice. For example, along the brushy streamside habitat of Beaver Creek Canyon, 15 *R. m. dychei* were live-trapped in late June 1968, along with 18 *M. pennsylvanicus*, 25 *P. maniculatus*, 10 *Zapus hudsonius*, and one juvenile *Neotoma cinerea*. Five of these small rodents were collected near Hot Springs on 4 September 1968, on grassy ridges and in apple orchards that flank the Fall River.

At higher elevations, individuals were collected in erosional ditches, hayfields, and along the interface of forested areas. J. A. King obtained two females in snaptraps placed under a log and beneath an overhanging creek bank in a spruce-filled canyon southeast of Hill City, and he took 12 additional harvest mice in a three-week period (28 December 1945 to 15 January 1946) from a gopher mound located in an upland pasture in the same general area.

Only eight of 56 *R. megalotis* from the Black Hills area that are housed in the Museum of Natural History are adult females, so reproductive data are meager. In 1968, harvest mice in Wind Cave National Park evidently bred from early spring to late summer. A pregnant female was live-trapped and released in Beaver Creek Canyon on 27 June, and a lactating female was taken there on 2 July. Two pregnant females, one carrying two embryos that were 19 in crown-rump length and the other with four embryos (10 in crown-rump length), were obtained in the same canyon on 26 July. Two additional pregnant females, each carrying four embryos that were six in crown-rump length, were captured near the Park Headquarters on 30 August and 1 September. In other parts of the Hills, young of the year were apparent in late May to late August. Testes of 11 summer-taken males were 7.2 (6-8) in length.

Juvenal pelage of this mouse is short, fine and dark grayish-brown in color (Jones and Mursaloglu, 1961:14). Five adults from Fall River County taken in mid-June 1967 were undergoing the process of molt as evidenced by new hairs over the anterior three-quarters of the sides and dorsum, and by the line of demarcation between fresh summer pelage and the worn winter pelage still present on the rumps of these individuals. Other specimens obtained at this time either were in fresh summer pelage or showed no signs of pelage replacement. Three individuals captured in Wind Cave National Park late in August 1968 were molting simultaneously over most parts of the body from the summer pelage to

the longer and more dense winter pelage.

Harvest mice from the Black Hills are parasitized externally by ticks, *Ixodes spinipalpis* Hadwen and Nuttall, furmites, *Dermacarus hypudaei* (Koch), laelaptid mites, *Androlaelaps fahrenholzi* (Berlese) and *Ornithonyssus bacoti* (Hirst), chiggers, *Euschoengastia fasolla* Brennan and Beck, fleas, *Malaraeus telchinum* (Rothschild) and *Monopsyllus wagneri* (Baker), and an unidentified Anopluran louse that is represented in collections only by the nymph stage.

The preponderance of males in collections from the Black Hills invalidates any attempts to test for secondary sexual dimorphism in *R. megalotis*. When studying harvest mice on the Great Plains, Jones and Mursaloglu (1961:12-13) found that the females are, on the average, larger than males in all external and several cranial dimensions. However, individual variation greatly exceeded secondary sexual variation and statistically significant differences were lacking. A pattern of variation in coloration or size in the Hills was not readily discernible in the present study.

The remarkable uniformity in pelage color of *R. megalotis* over a considerable geographic range also was noted by Jones and Mursaloglu (1961:16). Most grassland cricetine species on the Great Plains have a dark eastern population and a pale western population. Environmental conditions along riparian habitats across the plains are somewhat similar to conditions of more eastern habitats, possibly lessening differential selection pressures of *R. megalotis* in comparison to that incurred by nonriparian grassland cricetines (*loc. cit.*). No significant geographic variation in color or size is evident in specimens examined from areas surrounding the Hills in South Dakota and Wyoming (Table 15). Cranial measurements were taken in the manner described by Hooper (1952:9-11). Additional external and cranial measurements (not included on Table 15) of 16 adults from the Hills are: tail length, 62.5±9.47; hind foot length, 16.6±0.81; ear length, 13.6±1.33; interorbital constriction, 3.2±0.13; length of incisive foramen, 4.4±0.15; depth of skull, 7.8±0.18.

Specimens examined (96).—SOUTH DAKOTA: *Meade County:* Black Hawk, 1 (AMNH). *Pennington County:* Rapid City, 8 (SDMT); Moon, 22 mi W Hill City, 6200 ft, 1; 3-4 mi SE Hill City, 53-5400 ft, 22 (UMMZ); Spring Creek, 4 mi ENE Rockerville, 3600 ft, 1 (UMMZ). *Custer County:* Roby Canyon, 2 mi N, 22 mi W Custer, 5200 ft, 2; 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; 3 mi N Pringle, 1 (UMMZ); 5 mi N, 2 mi E Wind Cave, Wind Cave National Park, 4200 ft, 1; 1.5 mi N, 0.5 mi W Wind Cave, Wind Cave National Park, 3250 ft, 1; Beaver Creek Canyon, Wind Cave National Park, 4200 ft, 13; Headquarters, Wind Cave National Park, 4100 ft, 5; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 12; Wind Cave National Park, 5 (UMMZ); unspecified locality, 1 (UMMZ). *Fall River County:* 5.5 mi E Minnekahta, 4000 ft, 1; 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 9; 1 mi N, 5.5 mi E Hot Springs, 3400 ft, 2; 1 mi N, 6 mi E Hot Springs, 3400 ft, 3; Hot Springs, 1 (UMMZ); 4 mi E Hot Springs, 3400 ft, 1; 2 mi S, 2 mi E Hot Springs, 3600 ft, 1.

WYOMING: *Crook County:* 1.5 mi NW Sundance, 5000 ft, 3.

Additional records.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB).

Peromyscus leucopus aridulus Osgood

White-footed Mouse

Peromyscus leucopus aridulus Osgood, 1909, N. Amer. Fauna, 28:122, 17 April (type locality, Fort Custer, Big Horn Co., Montana).

The white-footed mouse occurs throughout the northeastern two-thirds of North America. The distribution of *Peromyscus leucopus* across the arid Great Plains closely approximates the dendritic pattern of mesic deciduous communities that follow major drainage systems. The species is relatively uncommon in the Black Hills. It inhabits the notably discontinuous deciduous woodland formations up to 6100 feet, although it is more abundant below 5000 feet. No specimens are at hand from Fall River County, but white-footed mice probably occur there. Although this mouse has been taken in the Hills only

TABLE 15.—Geographic variation in selected color, and external and cranial measurements of adult *Reithrodontomys megalotis* from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance	Total length	Weight	Greatest length of skull	Zygomatic breadth	Rostral length	Length of maxillary tooth-row
16 (14♂, 2♀)				Black Hills, South Dakota and Wyoming						
Mean	27.2	48.3	27.7	23.9	138.7	11.9	21.1	10.7	7.3	3.3
SD	±3.02	±0.22	±0.12	±0.21	±8.35	±1.14	±0.54	±0.41	±0.37	±0.10
16 (14♂, 2♀)				Harding County, South Dakota						
Mean	27.1	47.4	26.3	25.9	139.7	12.0	21.3	10.9	7.4	3.4
SD	±3.79	±0.23	±0.16	±0.32	±9.53	±1.32	±0.37	±0.31	±0.22	±0.09
3 (3♂, 0♀)				20 mi N Long Valley, Washabaugh Co., South Dakota						
Mean	26.2	48.5	27.3	24.2	143.0	12.8	20.9	10.5	7.1	3.3
SD	±2.93	±0.13	±0.20	±0.07	±2.00	±1.18	±0.66	±0.39	±0.32	±0.10
4 (3♂, 1♀)				Oelrichs and Edgemont, Fall River Co., South Dakota						
Mean	26.0	48.1	26.9	25.0	137.6	11.0	21.1	10.8	7.2	3.2
SD	±2.16	±0.15	±0.12	±0.14	±8.08	±2.22	±0.61	±0.12	±0.39	±0.08
26 (17♂, 9♀)				Southeast of Martin, Bennett Co., South Dakota						
Mean	26.3	47.8	27.2	24.9	135.0	13.2	20.9	11.0	7.2	3.3
SD	±2.98	±0.23	±0.12	±0.23	±4.50	±2.11	±0.47	±0.24	±0.27	±0.10
8 (4♂, 4♀)				Campbell County, Wyoming						
Mean	27.7	49.1	27.4	23.4	140.7	12.5	21.3	10.8	7.3	3.4
SD	±2.56	±0.19	±0.13	±0.10	±6.90	±3.27	±0.76	±0.32	±0.40	±0.11
8 (4♂, 4♀)				Platte, Laramie, and Niobrara counties, Wyoming						
Mean	26.6	50.0	27.1	22.9	140.6	12.0	21.4	11.0	7.4	3.4
SD	±3.10	±0.19	±0.17	±0.14	±9.62	±1.43	±0.58	±0.29	±0.25	±0.18

from mid-June to mid-August, it is active the year around and does not hibernate. J. A. Allen (1894a:325) first reported white-footed mice from the Hills under the name *Sitomys americanus arcticus* (see below).

Big Spearfish Canyon extends from Savoy, where the streambed elevation is about 5000 feet, northward, emerging from the Black Hills at Spearfish (3600 feet). Spearfish Creek courses below massive cliffs, with luxuriant vegetation (bur oak, American elm, boxelder, green ash, and deciduous shrubbery) on the canyon floor. Sixteen (11 males and five females) *P. leucopus* were taken in the underbrush of this riparian woodland in early August 1967. Vanocker Canyon arises on the southeast slopes of Deadman Mountain (4800 feet) and extends northeastward, emerging at Sturgis (3600 feet). Five individuals (four males and one female) were obtained in this canyon on 28 June 1967, and two more (one of each sex) were collected there on 15 August 1967. These mice were trapped in brush in a pasture that bordered an aspen grove, and in a mixed oak, pine, and aspen woodland.

Nine *Peromyscus leucopus* (five males and four females) were captured in the Central Basin, northeast of Custer, in late June 1967. These were taken in aspen woodlands bordering Iron and Grizzly creeks; the woodland contained much undergrowth, fallen logs, deciduous shrubbery and rock outcroppings. *Eutamias minimus, Peromyscus maniculatus, Clethrionomys gapperi, Microtus longicaudus,* and *M. pennsylvanicus* are associates of *P. leucopus* in the Hills.

White-footed mice also inhabit alluvial wooded bottomlands of drainages in the Red Valley and foothills. Specimens collected along Squaw Creek in late July 1894 by W. W. Granger were taken in an area that, "is wooded with aspen, willows, boxelders and other deciduous trees" (J. A. Allen, 1895a:261). Granger also captured eight *P. leucopus* well out on the prairie east of the Black Hills, about seven miles southwest of the mouth of Spring Creek. This site is mentioned as a further example of the restricted habitat of *P. leucopus* on the plains. Spring Creek was "bordered by boxelders, cottonwoods, plum thickets, willows, wild currants, and rank weeds and grass" at the time of Granger's visit (*loc. cit.*).

Throughout its range in the Black Hills, the white-footed mouse is sympatric with the deer mouse. These two species are often taken side-by-side in the same trapline (see account of *Peromyscus maniculatus*) and are frequently difficult to differentiate. For example, J. A. Allen (1895a:268) listed 39 specimens of *Peromyscus leucopus* from Custer and 20 from Squaw Creek. He noted that a few specimens presented a decided fulvous or reddish wash, and that one specimen (AMNH 9370) approached the characteristic "fulvous tint of *nebracensis*" [*P. maniculatus*]. Allen later (1899: 15) assigned all of these specimens to a new subspecies, "*Peromyscus texanus subarcticus* [*P. m. artemisiae*]," stating "Black Hills specimens are not at all typical, some of them decidedly approaching *P. t. nebracensis,* while others are quite like the Montana and Saskatchewan examples." Only 10 of the 59 specimens listed by Allen are actually *P. leucopus,* the remainder being *maniculatus* (including AMNH 9370). Externally, white-footed mice are larger in body size, have longer tails and hind feet, and the summer pelage is somewhat duller, with a less distinctly bicolored tail, in comparison with deer mice. Subadults of the former species are easily confused externally with adults of the latter, but the larger, more robust skull of *P. leucopus,* coupled with age determination by degree of tooth wear, readily resolves this dilemma.

Three of six adult female *P. leucopus* from the Hills, for which reproductive data are available, showed signs of reproductive activity. One taken northeast of Custer on 26 June 1967 carried six embryos that were 3 in crown-rump length.

Another, obtained southwest of Sturgis on 28 June 1967, was lactating and had five placental scars present in the reproductive tract. The third, captured south of Sturgis on 15 August 1967, had four placental scars. The average length of testes of 11 adult males collected in the summer was 11.8 (10-13).

Many adult white-footed mice taken in late June and early July were molting over the dorsum and sides, whereas other individuals already were in fresh summer pelage. Juveniles have soft gray fur. Two subadults from northeast of Custer (19 June 1967) were undergoing post-juvenal molt in which new brown hairs were emerging along the sides, whereas the dorsum still was furred in the grayish juvenal pelage.

Examination of 26 *P. leucopus* (16 males and 10 females) from the Black Hills revealed no apparent secondary sexual variation in coloration or in external and cranial measurements, nor was a pattern of variation in these parameters discernible in the Hills populations.

Specimens from the Black Hills, and adjacent areas to the west in Crook County, Wyoming, are darker in average tone of color, and much smaller in most external and cranial dimensions when compared to populations on the South Dakotan plains (Tables 16 and 17). The small size of the Black Hills representatives has been a source of past misidentifications.

Peromyscus leucopus probably extended its range westward on the Great Plains along major drainage systems in mesic Post-Wisconsin times. The presently isolated segments formerly were part of a more or less continuous and

Table 16.—Geographical variation in coloration of the mid-dorsal pelage of adult *Peromyscus leucopus* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
26 (16♂, 10♀)		Black Hills, South Dakota and Wyoming		
Mean	26.7	48.4	27.4	24.2
SD	±3.60	±0.28	±0.17	±0.17
6 (5♂, 1♀)		Crook County, Wyoming		
Mean	26.2	48.4	28.3	23.3
SD	±1.37	±0.22	±0.20	±0.12
5 (4♂, 1♀)		Washabaugh County, South Dakota		
Mean	26.4	48.5	27.0	24.5
SD	±2.86	±0.22	±0.17	±0.26
15 (7♂, 8♀)		Todd County, South Dakota		
Mean	26.9	47.3	27.5	25.2
SD	±2.47	±0.31	±0.20	±0.24
7 (3♂, 4♀)		Harding County, South Dakota		
Mean	27.4	49.5	27.0	23.5
SD	±2.39	±0.32	±0.16	±0.21
17 (7♂, 10♀)		Bennett County, South Dakota		
Mean	27.5	49.5	26.4	24.1
SD	±3.25	±0.37	±0.22	±0.19
22 (11♂, 11♀)		Cherry County, Nebraska		
Mean	30.1	49.5	26.6	23.9
SD	±3.26	±0.26	±0.18	±0.17

TABLE 17.—Geographic variation in selected external and cranial measurements of adult *Peromyscus leucopus* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Tail length	Hind foot length	Ear length	Greatest length of skull	Zygomatic breadth	Rostral length	Length of incisive foramen	Skull depth
38 (25♂, 13♀)				Black Hills, South Dakota and Wyoming					
Mean	164.2	70.6	20.7	16.5	26.4	13.6	9.8	5.4	9.6
SD	±12.98	±10.72	±0.33	±1.29	±0.82	±0.54	±0.49	±0.25	±0.28
6 (5♂, 1♀)				Crook County, Wyoming					
Mean	171.5	75.3	21.8	16.5	26.2	13.7	9.5	5.3	9.5
SD	±13.69	±5.95	±0.75	±1.52	±1.19	±0.67	±0.75	±0.43	±0.21
5 (4♂, 1♀)				Washabaugh County, South Dakota					
Mean	175.4	77.2	21.4	17.0	27.2	14.1	10.2	5.5	9.8
SD	±11.10	±4.32	±0.55	±1.22	±0.84	±0.56	±0.58	±0.27	±0.18
16 (8♂, 8♀)				Todd County, South Dakota					
Mean	172.2	74.9	21.8	17.1	27.2	14.1	10.2	5.6	9.8
SD	±13.41	±6.51	±0.75	±1.23	±1.10	±0.63	±0.69	±0.32	±0.25
7 (3♂, 4♀)				Harding County, South Dakota					
Mean	184.4	77.4	21.1	16.7	27.7	14.7	10.5	5.5	10.0
SD	±8.42	±6.50	±0.61	±0.76	±0.45	±0.32	±0.28	±0.23	±0.22
17 (7♂, 10♀)				Bennett County, South Dakota					
Mean	176.3	77.8	21.3	16.0	27.2	14.4	10.3	5.5	9.9
SD	±9.95	±8.59	±0.86	±1.62	±0.97	±0.61	±0.54	±0.28	±0.32
34 (20♂, 14♀)				Cherry County, Nebraska					
Mean	170.1	72.9	22.0	15.8	27.2	14.4	10.3	5.5	9.8
SD	±7.76	±4.57	±0.65	±0.73	±0.73	±0.51	±0.48	±0.23	±0.25

interbreeding population (Jones, 1964: 197). Currently, gene-flow between these limited populations probably is reduced or absent, and these populations presumably now are adapting to environmental conditions independently.

Measurements additional to those on table 17 of 38 white-footed mice from the Hills are: weight, 23.4±4.66; interorbital constriction, 4.2±0.14; and length of maxillary tooth-row, 4.0±0.15.

Specimens examined (62).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 1.5 mi S, 0.5 mi E Spearfish, 3800 ft, 7; Big Spearfish Canyon, 3 mi S Spearfish, 4200 ft, 6; Big Spearfish Canyon, 5 mi S, 2 mi W Spearfish, 4600 ft, 1; Big Spearfish Canyon, 9 mi S, 3 mi W Spearfish, 5000 ft, 2; 2 mi S Tinton, 6100 ft, 1; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 1; 2 mi W Nemo, 4700 ft, 2. *Meade County:* Vanocker Canyon, 2 mi S Sturgis, 2; Vanocker Canyon, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 5. *Pennington County:* 1 mi S, 8.5 mi W Rapid City, 1. *Custer County:* 5.75 mi N, 5.75 mi E Custer, 5220 ft, 9; Custer, 3 (1 USNM, 2 AMNH); Custer State Park, 1 (UMMZ); Squaw [Grace Coolidge] Creek, 3000 ft, 8 (7 AMNH, 1 FMNH); 0.25 mi N Otis, 2 (UMMZ).

WYOMING: *Crook County:* 15 mi ENE Sundance, 3825 ft, 9; Sundance, 2 (USNM).

Additional record.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB).

Peromyscus maniculatus nebrascensis (Coues)

DEER MOUSE

Hesperomys sonoriensis var. *nebrascensis* Coues, 1877, *in* Coues and Allen, Bull. U. S. Geol. Surv. Territories, 11:79, August (type locality restricted to Deer Creek, approximately five miles from its mouth, Converse Co., Wyoming, by Jones, Proc. Biol. Soc. Washington, 71:108, 16 July 1958).

Peromyscus maniculatus nebrascensis—Osgood, 1909, N. Amer. Fauna, 28:75, 17 April.

In the Black Hills, this ubiquitous cricetid is by far the most abundant and widely distributed of the mammalian

species. Although it is most common in grassy environs of the Red Valley and foothills, *P. maniculatus* occurs in a wide variety of habitats, including cultivated cropland, grazed or ungrazed pastureland, grassland meadows, marsh and stream borders, spruce and aspen woodlands, dense pine forests, and even among bare rock at the summit of Harney Peak (7240 feet), atop Devils Tower, and several hundred feet below ground surface in Wind Cave.

Dice (1939:5) estimated that the total population of *P. maniculatus* in the Black Hills in late summer of 1935 was between one and five million individuals. He indicated that deer mice occurred in the greatest abundance in dense and medium dense stands of western yellow [ponderosa] pine in densities of 932 and 894 mice per square mile, respectively (*op. cit.*:2, Table 1). However, Dice (1939:1) based his estimates on only 39 specimens and erroneously assumed that the Black Hills population was isolated to a large extent. Due to poor trapping results in grasslands near Rapid City and south of Hot Springs, Dice did not trap in grassland, pasture, or cultivated fields in other parts of the Hills (*op. cit.*:3) assuming that no deer mice occurred in these areas (*op. cit.*:4).

My own investigations indicate that, although deer mice are omnipresent in the Black Hills, the highest population densities are attained in those environs dominated by graminoid vegetation. For example, in a five-day period (13-18 June 1967) 82 deer mice were captured near Minnekahta in arid pastureland of the Red Valley (see account of *Microtus ochrogaster* for a description of the area). In approximately 2000 trap-nights in the summer of 1968, 315 *P. maniculatus* were taken in the grassy uplands and semi-grassy canyon systems of Wind Cave National Park. On 27 August alone, 66 deer mice were captured in 150 trap-nights. Most of these specimens were discarded after being examined for ectoparasites and autopsied for reproductive data. Because quadrat sampling methods were not used in the current study, calculations of population size were not attempted, but, it is certain that Dice's computations underestimated the number of deer mice in the Black Hills.

In the northern foothills and canyons, and along some drainages in the central section of the Black Hills, *P. m. nebrascensis* is ecologically sympatric with *P. leucopus* (see account of that species). I have taken both species within a few feet of each other, and even in the same trap, in Little Spearfish Canyon. However, *P. leucopus* is less common and is stenoecious, generally associating with elements of the eastern deciduous forest. Due to its occurrence in all available habitats, the deer mouse is closely associated with each of the other terrestrial mammals in the Hills region.

Deer mice captured in Wind Cave National Park in summer of 1968 were grouped into age classes based on tooth wear, general dimensions, and type of pelage. Of 315 individuals, there were 188 adults, 116 subadults, and 11 juveniles. Mice taken in July (97) and August (203) were further segregated by sex. In the following analysis of population composition, percentages for July are followed by those for August: adult males, 32.0, 32.0; adult females, 25.8, 28.1; subadult males, 19.6, 12.8; subadult females, 20.6, 22.7; juvenile males, 1.0, 3.4; juvenile females, 1.0, 1.0; The analysis indicated that about 40 percent of summer populations of *P. maniculatus* in the Black Hills are immature individuals.

This species may breed most months of the year in the Hills region, but adequate data are available only for the summer. J. A. King captured two pregnant females southeast of Hill City, one of which carried five embryos (14 March 1946) measuring three in crown-rump length, and the other containing two embryos (25 March 1946) measuring 23 in crown-rump length. On 5 April 1946, King obtained two gravid females north of Newcastle that each carried five embryos which had an average crown-rump length of 2 and 3, respectively.

Of 257 female *P. maniculatus* obtained in the summer from the Black Hills and autopsied, 48.3 percent showed indications of reproductive activity. Because many nearly-mature subadults carried fetuses, both adults and subadults were examined in this study. Of 48 females collected in June, 16 were pregnant, having an average of 5.2 (4-7) embryos that were 9.3 (4-19) in crown-rump length. Four placental scars were manifest in the reproductive tract of another individual, and seven females were lactating. The average length of testes of 67 males obtained in June was 9.0 (6-18). In July, 24 of 87 females were parturient, and carried 5.0 (4-9) fetuses; the average crown-rump length of the latter was 11.8 (2-25). Three other individuals had 4.3 (4-5) placental scars; a like number of females had swollen uteri, possibly indicating recent implantation. Twenty additional females were lactating. The average testicular length of 64 males taken in July was 9.6 (6-18). Of 97 females obtained between 16 and 31 August, only 11 were gravid, containing 4.6 (4-6) embryos with an average crown-rump length of 16.8 (6-27). Twelve other females had 4.3 (3-6) placental scars, and nine other individuals were lactating. Six females had swollen uteri. Seventy-two males captured in the same period had an average testicular length of 9.8 (7-17). In the first week of September, six of 25 females contained 4.3 (3-6) young each that had an average crown-rump length of 16.8 (8-23). Three females had 5.7 (5-6) placental scars, and three other individuals were lactating. The average testicular length of 27 males obtained in the period 1 to 7 September was 9.4 (5-18). Analysis of reproductive data on a monthly basis masks short-termed fluctuations. For example, the percentages of pregnant individuals encountered over four successive two-week periods were: 1 to 15 June, 40.0 percent of 25 females; 16 to 30 June, 26.1 percent of 23 females; 1 to 15 July, 36.6 percent of 41 females; and 16 to 31 July, 19.6 percent of 46 females.

Adults molting from winter to summer pelage were taken as early as 10 June, but maximal time of pelage replacement occurred from late June to mid-July. Osgood (1909:19) indicated that there is but one complete annual change in pelage of adult *Peromyscus* and that the process commences near the head, progressing caudad. Molting individuals trapped in late August and early September appeared to be acquiring the characteristic long, dense pelage of winter, and apparently were undergoing a second seasonal molt. The high reproductive rate of deer mice results in many individuals of different ages occurring simultaneously in the same area throughout warmer months, thus complicating interpretation of seasonal aspects of molt. Subadults undergoing post-juvenal molt were observed in all periods. The slate-gray juvenal pelage is replaced by brownish to buffy hairs that first occur along the upper portion on each side.

Twenty-two kinds of ectoparasites were harbored by *P. maniculatus* from the Black Hills: two lice, *Hoplopleura hesperomydis* (Osborn) and *Polyplax auricularis* Kellogg and Ferris; three chiggers, *Euschoengastia setosa* (Ewing), *Psuedoschoengastia farneri* Lipovsky, and *Xenacarus plumosus* (Greenberg); four ticks, *Dermacentor andersoni* Stiles, *Ixodes kingi* Bishopp, *I. spinipalpis* Hadwen and Nuttall, and individuals of the *I. ochotonae-angustus* complex; six mites, *Androlaelaps fahrenholzi* (Berlese), *Dermacarus hypudaei* (Koch), *Eulaelaps stabularis* (Koch), *Laelaps microti* (Ewing), *Ornithonyssus bacoti* (Hirst), and members of the genus *Hirstionyssus;* and seven fleas, *Monopsyllus wagneri* (Baker), *M. eumolpi* (Rothschild), *Malaraeus telchinum* (Rothschild), *Orchopeas leucopus* (Baker), *O. sexdentatus* (Baker), *Catallagia decipiens* (Rothschild), and *Epitedia wenmanni* (Rothschild).

Comparison of 56 male and 42 female deer mice from the Black Hills revealed

no significant secondary sexual dimorphism in external or cranial measurements, although females are slightly larger in most dimensions. Males are paler in tone (29.8±4.12) and greater in reflectance of reds (50.6±0.36) than are females (27.4±4.85 and 49.5±0.28, respectively); however, there is considerable variability in each of these parameters.

Peromyscus maniculatus is quite variable in color and in external and cranial dimensions in the Black Hills; this is probably due to a greater divergence in topography, habitat, and edaphic factors in the Hills than in the surrounding prairie. Dice (1941:16) noted a general tendency for this species to increase in size westwardly over the Great Plains, and indicated (1942:9) that the presence of the Black Hills does not affect this trend in any significant manner. Deer mice in the Hills are intermediate in size between eastern, northern, and western populations, but are assignable to the western subspecies (Table 18). *Peromyscus maniculatus nebrascensis* differs from *P. m. luteus* to the east in being larger externally and cranially, and in being darker dorsally (Fig. 13 and Table 19). Osgood (1908:78) noted that, although typical *nebrascensis* average decidedly larger than typical *luteus,* individual variation in each race is great enough to allow overlap in the range of various parameters. For example, he regarded five of 13 specimens from Elk Mountain as resembling *luteus,* and the other eight as resembling *nebrascensis.* Occasional high frequencies of paler and smaller mice in the foothills and peripheral areas may be expected due to gene exchange with populations of the surrounding plains. Specimens from Rapid City, for example, approach the dimensions of *luteus* rather than *nebrascensis.*

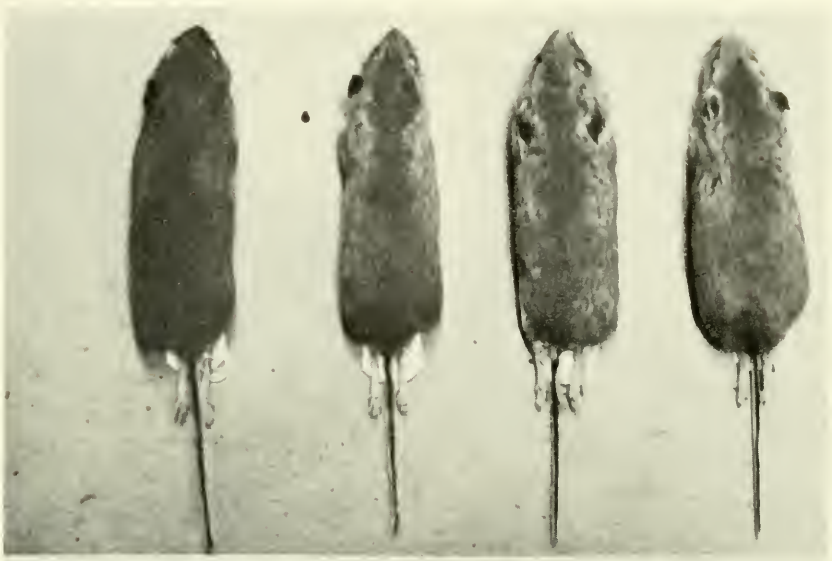
Stebler (1939:391-392) and Dice (1942:1-10) both discussed the correlation between soil color and pelage color of *P. maniculatus* in the study area. In general, the soils of the Black Hills are dark in color, varying from reddish to blackish brown. When comparing habitats of the Badlands with those of the Black Hills, Dice (1942:6) stated: "On the forested Black Hills, on the contrary, the variation from place to place in soil color is relatively slight, and there is only a small amount of variability in the color of deer-mice." In actuality, soils of the Hills are exceedingly diverse in coloration. For example, the two soils collected south of Spearfish (Table 20) were within 20 yards of one another; sample A was obtained mid-way up a steep slope, and sample B was taken at the base of the slope. Soils from near Rapid City register abnormally pale in tone due to a high gypsum content that increases reflection properties of the soil. This great diversity in coloration of soils invalidates comprehensive correlations between pelage and soil hues, unless a soil sample is taken at each site of capture throughout the entire Hills region. Collectively, soils of the Red Valley "racetrack" differ significantly from those of the Limestone Plateau and Central Basin, being paler in tone and reflecting reds more intensely. Soils of the Central Basin average somewhat paler in tone than those of the Limestone Plateau, but otherwise they are fairly similar.

Peromyscus maniculatus in the Black Hills is much darker on the average than either the small "ochraceous-buff" race on the arid plains south and east of the Hills, or the large "reddish" race on the sandy soils of eastern Wyoming (Fig. 13 and Table 19). Collectively, specimens from the southern Hills (especially from southwest of Minnekahta) are, on the average, paler than those from the northern section, and specimens from the western part (especially from the vicinity of Ditch Creek, Beaver Creek, Four Corners, and Buckhorn) have greater reflection of reds than individuals from the eastern Hills.

Measurements additional to those given in Table 18 for 98 adult specimens from the Black Hills are: zygomatic

TABLE 18.—Geographic variation in selected external and cranial measurements of adult *Peromyscus maniculatus* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Tail length	Hind foot length	Ear length	Weight	Greatest length of skull	Rostral length	Skull depth	Length of incisive foramen	Length of maxillary tooth-row
				P. m. luteus, Bennett County, South Dakota						
33 (22 ♂, 11 ♀)										
Mean	147.3	60.2	18.3	15.5	20.0	24.4	9.2	8.9	5.1	3.6
SD	±8.59	±5.04	±1.61	±1.06	±3.31	±0.69	±0.43	±0.26	±0.24	±0.19
				P. m. nebrascensis, Black Hills, South Dakota and Wyoming						
98 (56 ♂, 42 ♀)										
Mean	150.2	61.4	19.1	16.7	21.8	24.9	9.7	9.1	5.3	3.7
SD	±16.56	±6.20	±1.01	±1.15	±3.05	±0.68	±0.39	±0.29	±0.28	±0.14
				P. m. nebrascensis, Harding County, South Dakota						
23 (13 ♂, 10 ♀)										
Mean	152.0	61.5	18.9	16.1	22.6	25.1	9.7	9.1	5.2	3.7
SD	±10.64	±5.51	±0.87	±1.47	±3.53	±0.64	±0.38	±0.25	±0.17	±0.15
				P. m. nebrascensis, Converse, Niobrara, and Weston counties, Wyoming						
56 (34 ♂, 22 ♀)										
Mean	157.6	64.1	19.5	17.8	23.5	25.3	9.8	9.1	5.3	3.7
SD	±11.02	±7.03	±1.01	±1.53	±3.71	±0.71	±0.43	±0.22	±0.25	±0.16



	P M NEBRASCENSIS BLACK HILLS	P M NEBRASCENSIS HARDING CO, S D.	P M NEBRASCENSIS EASTERN WYOMING	P M LUTEUS BENNETT CO, S D
TONE	28.2•4.58	30.4•2.93	33.1•5.15	34.8•4.57
%RED	49.8•0.34	50.7•0.25	51.0•0.25	48.2•0.30
%GREEN	26.5•0.19	25.3•0.21	26.1•0.16	27.8•0.15
%BLUE	23.7•0.19	24.0•0.11	22.9•0.14	24.0•0.19

FIG. 13. Geographic variation in coloration of the mid-dorsal pelage of four groups of adult deer mice collected during the summer. *Peromyscus maniculatus nebrascensis* averages much darker in tone than the "ochraceous-buff" race, *P. m. luteus,* to the south and east, and specimens of *P. m. nebrascensis* from the Black Hills average much darker than either the dark form from Harding County, South Dakota, or the "reddish" form that inhabits sandy soils of eastern Wyoming.

breadth, 13.1±0.40; and interorbital constriction, 3.9±0.26.

Specimens examined (778).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 5 mi S, 2 mi W Spearfish, 4600 ft, 2; Big Spearfish Canyon, 6 mi S, 2 mi W Spearfish, 4600 ft, 1; Tinton, 5900 ft, 21; 2 mi S Tinton, 6100 ft, 37; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 1; Little Spearfish Canyon, Savoy, 4 (USNM); Deadwood, 1 (USNM); Roubiax Lake, 2 (FMNH); Dumont, 1 (USNM); 2 mi W Nemo, 4700 ft, 6; 1 mi E Nemo, 4700 ft, 2; 3 mi E Nemo, 4650 ft, 1; Boxelder Creek Canyon, 2 (NRW); Steamboat Rock Campground, 3 (NRW); Jim Creek, east Merritt, 1 (NRW). *Meade County:* 3 mi S, 0.5 mi W Sturgis, 4400 ft, 1; 6 mi S, 1.5 mi W Sturgis, 4600 ft, 2; Black Hawk, 9 (AMNH). *Pennington County:* 1.5 mi W Rochford, 1 (UMMZ); south slope Norris Peak, 1 (NRW); Castle Creek, 6500 ft, 1 (UMMZ); Bald Hills, Pactola, 1 (USNM); 8 mi NE Rapid City, 3 (UMMZ); 4 mi N Rapid City, 7 (AMNH); 3 mi N Rapid City, 3 (NRW); 2 mi N, 3 mi E Rapid City, 2; Rapid City, 65 (3 UMMZ, 3 USNM, 48 NRW, 3 SDMT); Dark Canyon, 1 mi S, 4 mi W Rapid City, 15 (AMNH); 4 mi SE Rapid City, 2 (UMMZ); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 56; Beaver Creek, 3 mi N, 9 mi W Deerfield, 6500 ft, 8; 3 mi N, 7 mi W Deerfield, 6900 ft, 3; Redfern, 9 (USNM); Rocky Mountain Range Experimental Station, McVey Burn, 2 (NRW); NE Sheridan Lake, 2 (NRW); Spring Creek Canyon, 3 (NRW); Wild Irishman Gulch, 2 (NRW); 3 mi S, 1 mi W Rockerville, 6; Spring Creek, south Rapid City, 6 (MHM); 4 mi NW Hill City, 4 (UMMZ); Moon, 22 mi W Hill City, 6200 ft, 4; Ditch Creek, 14 mi W Hill City, 6400 ft, 22; 3-4 mi SE Hill City, 5300-5400 ft, 38 (UMMZ); 5 mi SE Hill City, 1 (UMMZ); 2 mi W Oreville, 5500 ft, 1 (UMMZ); 17 mi NW Custer, 3

TABLE 19.—Geographic variation in coloration of the mid-dorsal pelage of adult *Peromyscus maniculatus* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
33 (22 ♂, 11 ♀)	*P. m. luteus*, Bennett County, South Dakota			
Mean	34.8	48.2	27.8	24.0
SD	±4.57	±0.30	±0.15	±0.19
55 (34 ♂, 21 ♀)	*P. m. nebrascensis*, Converse, Niobrara, and Weston counties, Wyoming			
Mean	33.1	51.0	26.1	22.9
SD	±5.15	±0.25	±0.16	±0.14
23 (13 ♂, 10 ♀)	*P. m. nebrascensis*, Harding County, South Dakota			
Mean	30.4	50.7	25.3	24.0
SD	±2.93	±0.25	±0.21	±0.11
84 (47 ♂, 37 ♀)	*P. m. nebrascensis*, Black Hills, South Dakota and Wyoming			
Mean	28.2	49.8	26.5	23.7
SD	±4.58	±0.34	±0.19	±0.19

TABLE 20.—Color of dry samples of surface soil from the Black Hills (arranged within counties in order of decreasing tone of color).

Locality	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
Lawrence County				
2 mi W Nemo	46.0	48.9	28.3	22.8
2 mi S Spearfish (A)	36.5	56.2	23.3	20.5
3 mi S Nemo	31.0	51.6	25.8	22.6
3 mi S Spearfish (B)	25.5	52.9	25.5	21.6
Timon Campgrounds	21.0	47.6	26.2	26.2
Meade County				
3 mi SW Sturgis	39.5	59.5	21.5	19.0
Pennington County				
Rapid City	97.5	49.7	27.2	23.1
3 mi SE Hill City	28.0	48.2	26.8	25.0
Bald Hills	27.5	49.1	27.3	23.6
Beaver Creek Valley	21.0	47.6	26.2	26.2
Custer County				
Keystone	50.0	46.5	28.7	24.7
Wind Cave National Park	32.0	51.6	26.6	21.9
Roby Springs	24.5	49.0	26.5	24.5
Custer	20.5	48.8	26.8	24.4
Flynn Creek	16.5	48.5	27.3	24.2
Fall River County				
Hot Springs	36.0	59.7	20.8	19.4
1 mi SW Minnekahta	32.0	60.9	21.9	17.2

(UMMZ); 16 mi NW Custer, 1 (UMMZ); Harney Peak, 7240 ft, 4 (UMMZ); unspecified locality, 9 (1 NRW, 3 SDMT, 5 UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 12 (FMNH); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 8; 5.75 mi N, 5.75 mi E Custer, 5220 ft, 19; Roby Springs, 4 mi N, 22 mi W Custer, 5400 ft, 2; Roby Canyon, 2 mi N, 22 mi W Custer, 5200 ft, 4; Squaw [Grace Coolidge] Creek, 14 (10 AMNH, 4 FMNH); Custer, 35 (32 AMNH, 3 FMNH); Harney National Forest, 3-5 mi E Custer, 3 (UMMZ); 4 mi SW Custer, 9; Lightning Creek, 8 mi SW Custer, 1 (UMMZ); 4 mi NE Otis, 1 (UMMZ); 3 mi N Pringle, 5000 ft, 2 (UMMZ); Campbell's Ranch, Elk Mountain, 4800 ft, 14 (USNM); Wind Cave National Park, 10 (1 UW, 8 UMMZ, 1 WCNP); 6 mi N, 1 mi E Wind Cave, Wind Cave National Park, 4400 ft, 1; 5 mi N, 2 mi E Wind Cave, Wind Cave National Park, 4200 ft, 4; Buffalo Corral, Wind Cave National Park, 4300 ft, 8; 2.5 mi N, 5 mi E Wind Cave, Wind Cave National Park, 3700 ft, 5; Beaver Creek Canyon, Wind Cave National Park, 4200 ft, 4; Wind Cave, Wind Cave National Park, 4; Headquarters, Wind Cave National Park, 4100 ft, 8; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 28; unspecified locality, 11 (UMMZ). *Fall River County:* 1 mi N, 6 mi E Hot Springs, 3400 ft, 2; 1 mi N, 5.5 mi E Hot Springs, 3400 ft, 2; 5.5 mi E Minnekahta, 4050 ft, 4; 4 mi E Hot Springs, 3400 ft, 3; 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 72; 1.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 6; 1 mi S, 2 mi E Hot Springs, 3400 ft, 4; 2 mi S, 2 mi E Hot Springs, 3600 ft, 2; 4 mi S Hot Springs, 1 (UMMZ); 3 mi N, 2 mi E Edgemont, 3500 ft, 1; 8 mi S Hot Springs, 3 (UMMZ); Angostura Dam, 6.

WYOMING: *Crook County:* 6.5 mi SSE Alva, Bear Lodge Mountains, 2 (UMMZ); Devils Tower, flood plain Belle Fourche River, 3350 ft, 2 (USNM); 15 mi ENE Sundance, 3825 ft, 11; Sand Creek, 1 (UW); 3 mi NW Sundance, 5900 ft, 12; 2 mi NW Sundance, 11; 1.5 mi NW Sundance, 5000 ft, 1; Sundance, 10 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 2; 4 mi E Four Corners, 2; 9 mi N, 1 mi E Newcastle, 5; 6 mi N Newcastle, 1; 1 mi N Newcastle, 4800 ft, 11 (UMMZ); Newcastle, 12 (USNM).

Additional records.—SOUTH DAKOTA: *Pennington County:* Rochford (BB); Medicine Mountain, 6200-6300 ft (Dice, 1942:3). WYOMING: *Weston County:* Stockade Beaver Creek, 4300 ft (Dice, 1942:3).

Neotoma cinerea orolestes Merriam

BUSHY-TAILED WOODRAT

Neotoma orolestes Merriam, 1894, Proc. Biol. Soc. Washington, 9:128, 2 July (type locality, Saguache Valley, 20 mi W Sagauche, Saguache Co., Colorado).

Neotoma cinerea orolestes—Goldman, 1910, N. Amer. Fauna, 31:104, 19 October.

Neotoma grangeri J. A. Allen, 1894, Bull. Amer. Mus. Nat. Hist., 6:324, 7 November (type locality, Black Hills, Custer, Custer Co., South Dakota).

Bushy-tailed woodrats are boreal mammals of higher altitudes and latitudes of the northern and western United States. In the Black Hills, *Neotoma cinerea* occupies crevices in rocky outcrops, mine-shafts, and abandoned cabins from the boreal cap down through the transition zone to about 4000 feet. These rats are active the year around and are common throughout the study area. Vernon Bailey (1888:442) first noted this species in the Black Hills, indicating that its principal food seemed to be seeds of conifers and that large piles of gnawed cones often were scattered around entrances to woodrat dens.

Woodrats are most abundant among ledges and vertical crevices in rocky outcrops that form the steep sides of valley and canyon systems; examples are Beaver Creek and Ditch Creek valleys, and Big and Little Spearfish canyons. Such areas support growths of ponderosa pine and creeping juniper. At lower elevations, where rocky terrain is less common, buildings and other man-made facilities often are inhabited. Mine shafts and caves also are frequented; I have observed *N. cinerea* in Wind Cave at depths of 325 feet below ground surface, and 2300 feet from any known entrance of the cave.

This species sometimes is active in late afternoon and one individual was taken by J. A. King at 16:30 hrs (MST) southeast of Hill City on 29 March 1946. This large cricetid builds nests that are globular or cup-shaped masses composed of dry grass, moss, leaves, and other fibrous materials; these nests generally contain cones of pine and spruce, bones of various animals, and other debris. On 4 July 1967, I found a mandible of *Canis lupus* in a nest to the rear of Davenport Cave, and a subadult in Wind Cave

amassed numerous flashbulbs and candles within its nest.

Eight pregnant females taken in mid-June contained 3.6 (3-4) embryos that had an average crown-rump length of 32.1 (4-50). Three lactating females were captured in late July and two others were collected in August. A female obtained southwest of Sturgis on 14 August 1967 had six placental scars, and two others taken southwest of Lead in the same month had four placental scars each in the uterine walls. Testicular length of adult males varies seasonally. The average testicular length of four males taken in June was 21 (16-30); whereas that of two captured in July was 12 each, and that of two obtained in August was 6 and 7, respectively. Juveniles are common in collections made from mid-June through August. Two suckling young, which were only a few days old, were removed from the teats of a female taken in Davenport Cave on 26 June 1967; the young were nearly naked and darkly pigmented dorsally. Three suckling young obtained on 8 July from northeast of Deerfield were older and in fine, short juvenal pelage that was dark gray in color. Change from juvenal to subadult pelage was evident in many specimens collected in late July, and several adults were undergoing annual molt over the sides and rump in late July and early August. White, star-shaped spots were noted on the foreheads of many individuals, especially on subadults.

Chambers (1948:8) observed a red squirrel kill a woodrat in the northern Hills near Lead. A female *Neotoma* from west of Nemo and a male taken southwest of Sturgis harbored ticks of the *Ixodes ochotonae-augustus* complex. Individuals from southwest of Lead were parasitized externally by two ticks, *Ixodes spinipalpis* Hadwen and Nuttall, and *Dermacentor andersoni* Stiles, two mites, *Androlaelaps fahrenholzi* (Berlese) and *Haemogamasus ambulans* (Thorell), two fleas, *Orchopeas sexdentatus* (Baker) and *Monopsylus wagneri* (Baker), and a chigger, *Euschoengastia setosa* (Ewing).

Black Hills woodrats were described by J. A. Allen (1894a:324-325) as a separate species, *Neotoma grangeri,* based on a series of 14 individuals from Custer and two others from Glendale; 11 of these specimens were subadults. However, in his revision of the genus *Neotoma,* Goldman (1910:105) indicated that topotypes of *N. grangeri* did not differ from typical *N. c. orolestes,* a conclusion with which I concur.

Some secondary sexual variation is apparent among the Black Hills populations of *N. cinerea.* Females are paler in tone of color and greater in breadth of interorbital constriction and length of maxillary tooth-row, but males are slightly larger in all other measurements. Because individuals are quite variable, the sexes were not treated separately in subsequent analysis.

Although no overall pattern of variation in size is apparent, coloration of woodrats varies from place to place in the Hills. For example, specimens from Beaver Creek are paler in tone (29.5 ± 6.26), reflect reds (51.9 ± 0.27) more intensely, and greens (23.7 ± 0.13) and blues (24.2 ± 0.20) less intensely than do specimens from Ditch Creek (24.7 ± 3.96, 45.2 ± 0.27, 28.1 ± 0.15, and 26.5 ± 0.29, respectively). Specimens from other localities represent gradations between these extremes.

Neotoma cinerea orolestes differs from *N. c. rupicola* on the plains to the south and east in being darker and having somewhat larger external and cranial dimensions. Specimens from the Black Hills are on the average significantly darker in tone and reflect blues more intensely than do other representatives of *orolestes* from west and north of the Hills (Fig. 14 and Table 21), but there were no significant differences in external or cranial measurements between these populations. Specimens from 0.5 mi E Buckhorn, Weston Co., Wyoming, and a subadult female from the Angostura Dam, Fall River Co., South Dakota, are some-

FIG. 14. Geographic variation in coloration of the mid-dorsal pelage of three groups of summer-taken adult bushy-tailed woodrats. *Neotoma cinerea orolestes* averages much darker in tone than *N. c. rupicola*, and specimens of *N. c. orolestes* from the Black Hills average much darker than non-Black Hills representatives to the west and north.

what more pale than typical Black Hills representatives, but are still best referred to *orolestes*. Selected average external and cranial measurements of eight males and 15 females from the Black Hills are: total length, 359.1±20.67; tail length, 148.0±10.31; hind foot length, 40.6±2.12; ear length, 33.4±2.55; weight, 272.5±77.95; greatest length of skull, 48.3±1.82; zygomatic breadth, 25.8±1.06; mastoid breadth, 20.2±0.63; rostral length, 20.1±0.84; interorbital constriction, 5.9±0.28; length of incisive foramen, 11.2±0.63; length of maxillary tooth-row, 9.9±0.49; depth of skull, 16.5±0.61.

Specimens examined (134).—SOUTH DAKOTA: *Lawrence County:* Little Spearfish Canyon, 2 mi S, 13 mi W Lead, 6000 ft, 1; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 6000 ft, 14; Little Spearfish Canyon, Savoy, 4 (USNM); Annie Creek, Black Hills, 6500 ft, 1 (USNM); Deadwood, 2 (USNM); 2 mi W Nemo, 4700 ft, 2. *Meade County:* Vanocker Canyon, 3 mi S, 1 mi W Sturgis, 4600 ft, 1; Davenport Cave, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 3. *Pennington County:* Dark Canyon, 4 (AMNH); Diamond S Ranch, near Rapid City, 2 (UMMZ); Rapid City, 2 (1 NRW, 1 USNM); 15 mi SW Rapid City, 1 (NRW); 4.5 mi N, 2.5 mi E Deerfield, 4; Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 10; Ditch Creek, 14 mi W Hill City, 6400 ft, 10; 8 mi W Hill City, 7000 ft, 3 (UMMZ); Glendale, 2 (AMNH); Hill City, 1 (FMNH); Summit Peak, 3 mi SE Hill City, 5700 ft, 3 (UMMZ); Mushroom Rock, 4 mi SE Hill City, 5500 ft, 2 (UMMZ); Willow Creek, 4 mi SE Hill City, 5700 ft, 1 (UMMZ); unspecified locality, 1 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 1 (FMNH); Bull Springs, 2 mi N, 9 mi W Custer, 10 (UMMZ); Custer, 15 (2 USNM, 12 AMNH, 1 FMNH); Housing Area, Wind Cave National Park, 4100 ft, 2; Wind Cave National Park, 7 (1 USNM, 1 WCNP, 5 UMMZ); Otis, 1 (UMMZ); Elk Mountain, 2 (USNM); unspecified locality, 7 (UMMZ). *Fall River County:* Angostura Dam, 1.

WYOMING: *Crook County:* Devils Tower, 2 (USNM); Sand Creek, 1 (USNM); 15 mi N Sundance, 1. *Weston County:* 0.5 mi E Buckhorn, 6100 ft, 5; 4 mi E Four Corners, 4; 3 mi N Newcastle, 1 (UW).

Clethrionomys gapperi brevicaudus (Merriam)

RED-BACKED VOLE

Evotomys gapperi brevicaudus Merriam, 1891, N. Amer. Fauna, 5:119, 30 July (type locality, 3 mi N Custer, 6000 ft, Custer Co., South Dakota).

Clethrionomys gapperi brevicaudus—Bole and Moulthrop, 1942, Sci. Publ. Cleveland Mus. Nat. Hist., 5:153, 11 September.

The red-backed vole is distributed in boreal and montane coniferous forest and its successional stages, and in brushy riparian habitats of North America. It inhabits the boreal cap of the Black Hills down to elevations of 4600 feet, but is most numerous above 5200 feet. It is active the year around. Although common in the Hills, no specimens are at hand from Meade or Fall River counties.

Merriam named the subspecies, *brevi-*

TABLE 21.—Geographic variation in coloration of the mid-dorsal pelage of adult *Neotoma cinerea* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
23 (8♂, 15♀)	*N. c. orolestes*, Black Hills, South Dakota and Wyoming			
Mean	27.2	48.5	26.3	25.2
SD	±4.31	±0.36	±0.24	±0.23
21 (8♂, 13♀)	*N. c. orolestes*, eastern half of Wyoming, and Harding County, South Dakota			
Mean	37.0	49.6	27.0	23.4
SD	±8.16	±0.23	±0.26	±0.14
6 (3♂, 3♀)	*N. c. rupicola*, western Nebraska			
Mean	46.3	50.8	26.4	22.8
SD	±7.32	±0.18	±0.18	±0.05

caudus, on the basis of two specimens obtained near Custer on 18 and 21 July 1888. Bailey (1897:129) subsequently raised *brevicaudus* to specific rank, because: "Its range is isolated and widely separated from that of other members of the genus by open prairie country and a wide belt of Transition Zone." Bole and Moulthrop (1942:153) reestablished *brevicaudus* as a subspecies of *C. gapperi* on the basis of additional material. As presently understood, *brevicaudus* is restricted to the Black Hills.

Ecological sympatry of this vole with *Microtus longicaudus* and *M. pennsylvanicus* will be discussed later (see accounts of those species). *Clethrionomys* primarily is an inhabitant of spruce, birch, and aspen woodlands, but also frequents drier pine-clad slopes. Individuals generally are trapped near brush, woodpiles, boulders, fallen logs, or under low spreading branches of creeping juniper. For example, Bailey trapped the holotype beneath a log in a deciduous thicket and captured a second individual adjacent to a log in pine timber on top of a ridge (Merriam, 1891:119). I captured six voles in thickets of deciduous shrubbery along Spearfish Creek on 8 August 1967. Many additional specimens were taken in brushy riparian habitats such as those found along Iron, Grizzly, Goldrun, Boxelder, Beaver, and Ditch creeks; soggy bog-like soils frequently were encountered in these areas.

In addition to moist spruce-filled canyons and deciduous woodlands, red-backed voles also occupy rockslides, areas of secondary regeneration on burned over hillsides, or even areas of extreme exposure. In late November 1945, J. A. King trapped five *Clethrionomys* in bare rocky areas among pine needles and other debris at the summits of Harney (7242 feet) and Summit (5700 feet) peaks. Occasionally, this species is active during the day. A male was taken about 10:00 hrs (MDT) west of Hill City on 12 June 1965, and another was captured at 19:30 hrs (MDT) in Beaver Creek Valley on 1 July 1965. Along with the meadow and long-tailed voles, *Zapus hudsonius*, *Sorex cinereus*, *Peromyscus maniculatus*, and *Eutamias minimus* are associates of red-backed voles.

Adequate reproductive data applicable to the Black Hills population of *Clethrionomys* are available only for July. However, abundance of subadults in mid-June and of juveniles in late August indicate that several litters are pro-

duced annually. A subadult female taken along Ditch Creek on 10 June 1965 carried three embryos that had a crown-rump length of 4 each. Two adult females obtained about this time showed no signs of reproductive activity. The average length of testes of nine males obtained in June was 9.0 (7-10); corresponding measurements of five subadults were 7.8 (6-9). Eight of 15 adult females captured in July were pregnant; they had an average of 6.8 (5-9) embryos that were 10.1 (5-20) in crown-rump length. Testicular length of 12 males collected in July was 9.7 (7-11); that of three subadults was 8.3 (7-10). A lactating adult female was captured southwest of Rockerville on 19 August 1965 and testicular length of six adult males obtained in August was 6.8 (6-8). Strangely, observations concerning the occurrence of placental scars in *C. g. brevicaudus* are lacking in field notes of collectors, even though notations of this type are entered for all other species; perhaps placental scars are more ephemeral in red-backed voles than in other small mammals.

Winter pelage is longer and softer than that of summer and the reddish brown dorsal stripe is much more distinct. Adults taken in mid-June and early July frequently were molting into the short grayish- to reddish-brown summer pelage; new hairs were enshrouded beneath the overlying older pelage on both sides and dorsum. Because a distinctive moltline is not formed the process of pelage replacement is rather imperceptible. Fur of juveniles is more grayish in color than that of adults. Many subadults taken in summer were molting simultaneously over much of the body, whereas others had completed postjuvenal molt and were in fresh brownish pelage.

A male captured northeast of Custer on 19 June 1967 was infested with ticks, *Dermacentor andersoni* Stiles.

Comparison of 27 male and 22 female *C. g. brevicaudus* revealed no apparent secondary sexual dimorphism in coloration or in external and cranial dimensions, nor was a pattern of variation in these characters evident in the Black Hills. *Clethrionomys gapperi brevicaudus* differs significantly from *C. g. galei* to the west in Wyoming in having a shorter tail and ear, longer hind feet, a higher skull, and darker pelage that reflects reds more intensely (Table 22).

TABLE 22.—Geographic variation in coloration of the mid-dorsal pelage of adult *Clethrionomys gapperi* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
46 (24♂, 22♀)	*C. g. brevicaudus*, Black Hills, South Dakota and Wyoming			
Mean	21.2	55.8	23.1	21.1
SD	±2.19	±0.34	±0.29	±0.19
12 (6♂, 6♀)	*C. g. loringi*, Walsh County, North Dakota, Marshall County, South Dakota and Crow Wing County, Minnesota			
Mean	21.0	57.4	22.3	20.3
SD	±3.18	±0.28	±0.24	±0.14
23 (16♂, 7♀)	*C. g. galei*, Big Horn County, Wyoming			
Mean	23.4	54.0	24.1	21.9
SD	±2.25	±0.26	±0.19	±0.15

Clethrionomys gapperi brevicaudus also averages somewhat shorter in total length and greater in lengths of skull and rostrum, and in zygomatic and lambdoidal breadths (Table 23). From *C. g. loringi* to the north and east, *brevicaudus* differs significantly in longer hind feet, greater lambdoidal breadth and a higher skull; it is also smaller in total length and length of tail, and greater in lengths of ear, skull, and rostrum and in zygomatic breadth. Measurements additional to those given in table 23 for 49 adult red-backed voles from the Black Hills are: weight, 25.4±4.48; interorbital constriction, 3.9±0.13; length of incisive foramen, 4.9±0.26; length of maxillary tooth-row, 5.4±0.25.

Specimens examined (229).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 6 mi S, 2 mi W Spearfish, 4600 ft, 6; Tinton, 5900 ft, 1; 2 mi S Tinton, 6100 ft, 22; Deadwood, 1 (USNM); Dumont, 6100 ft, 5 (USNM); 2 mi W Nemo, 4700 ft, 4; Nemo, 4700 ft, 1. *Pennington County:* Jim Creek, east of Merritt, 1 (NRW); Rapid Creek, 1.5 mi W Rochford, 1 (UMMZ); Diamond S Ranch, near Rapid City, 1 (UMMZ); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 21; 3 mi N, 7 mi W Deerfield, 6900 ft, 1; 1 mi S, 2 mi E Deerfield, 6400 ft, 1; McVey Burn, 1 (NRW); 20 mi N Elk Mountain, 6000 ft, 2 (USNM); Ditch Creek, 14 mi W Hill City, 6400 ft, 3; Hill City, 1 (AMNH); Palmer Gulch, 3 mi SE Hill City, 5300-5400 ft, 11 (UMMZ); Willow Creek, Nelson's Place, 4 mi SE Hill City, 5300-5400 ft, 13 (UMMZ); Harney Peak, 5 mi SE Hill City, 7240 ft, 1 (UMMZ); Rockerville, 1 (UMMZ); 3 mi S, 1 mi W Rockerville, 3; Keystone, 1 (NRW); 17 mi NW Custer, 11 (UMMZ); 16 mi NW Custer, 22 (UMMZ); 16 mi SW Rapid City, 1 (UMMZ); unspecified locality, 2 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 9 (FMNH); 0.5 mi E Sylvan Lake, 6250 ft, 1 (UMMZ); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 1; 5.75 mi N, 5.75 mi E Custer, 5220 ft, 21; 3 mi N Custer, 6000 ft, 2 (USNM); Custer, 21 (18 AMNH, 3 FMNH); Bull Springs, 2 mi N, 9 mi W Custer, 7 (UMMZ).

WYOMING: *Crook County:* 3 mi NW Sundance, 5900 ft, 3; Rattlesnake Creek, 3 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6100 ft, 21; 12 mi SE Newcastle, 1 (UMMZ).

Microtus longicaudus longicaudus (Merriam)

LONG-TAILED VOLE

Arvicola (Mynomes) longicaudus Merriam, 1888, Amer. Nat., 22:934, October (type locality, Custer, 5500 ft, Custer Co., South Dakota).

Microtus (Mynomes) longicaudus—J. A. Allen, 1895, Bull. Amer. Mus. Nat. Hist., 7:266, 21 August.

The long-tailed vole occurs on the boreal cap of the Black Hills and inhab-

TABLE 23.—Geographic variation in selected external and cranial measurements of adult *Clethrionomys gapperi* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Tail length	Hind foot length	Ear length	Greatest length of skull	Zygomatic breadth	Rostral length	Lambdoidal breadth	Skull depth
49 (27♂, 22♀)	*G. g. brevicaudus*, Black Hills, South Dakota and Wyoming								
Mean	134.0	34.5	18.7	14.9	24.5	13.6	8.5	11.6	9.6
SD	±8.60	±3.37	±0.95	±1.63	±0.76	±1.49	±0.41	±0.36	±0.26
19 (11♂, 8♀)	*G. g. loringi*, Walsh County, North Dakota, Marshall County, South Dakota and Crow Wing County, Minnesota								
Mean	135.2	35.8	18.2	14.1	23.7	13.2	8.3	11.3	9.1
SD	±9.36	±3.69	±1.28	±1.13	±0.71	±0.64	±0.33	±0.22	±0.22
23 (16♂, 7♀)	*G. g. galei*, Big Horn County, Wyoming								
Mean	140.7	38.8	18.3	16.4	24.3	13.3	8.3	11.5	9.3
SD	±8.83	±3.72	±0.88	±1.26	±0.43	±0.32	±0.21	±0.19	±0.24

its riparian environs bordering cold streams that descend into the lower semiarid transition zone. It is widely distributed but none has been taken as yet in Fall River County. Although specimens have been obtained in the Hills as low as 4200 feet, *M. longicaudus* is most abundant at elevations above 6000 feet. The Black Hills population is isolated from other generally montane populations westward and southward in Wyoming. The species does not hibernate and individuals have been captured in all seasons.

A distinct pattern of ecological separation between *M. longicaudus* and *M. pennsylvanicus* is not readily discernible in the Hills. W. W. Granger wrote about them as follows, "I found these mice [*M. pennsylvanicus*] in the same localities as the other species [*M. longicaudus*]. Some were caught on a hillside which was covered with aspens, and the rest along the banks of a creek" (J. A. Allen, 1895a:267). Both species frequently are captured in the same trapline in the mesic Northern Hills. For example, a Sherman live-trap placed beneath the overhanging bank of Little Spearfish Creek in the Timon Campground obtained one *M. longicaudus* and one *M. pennsylvanicus* within an hour (19:30-20:30 hrs MDT) on 31 July 1968. Vegetation in the vicinity of the trap was composed of mosses, grasses, and deciduous shrubs.

At higher elevations, *M. longicaudus* ranges farther from riparian situations than does *M. pennslyvanicus*, which inhabits moist meadows and edges of spruce and aspen forest. In the latter habitat, long-tailed voles overlap *Clethrionomys gapperi*. At lower elevations, *M. longicaudus* is more restricted to streamside environments and lowland marshes of rushes, sedges, and cattails, or other moist areas of much brush and fallen logs. In these areas, *M. pennsylvanicus* ranges farther from riparian situations and is more tolerant of the drier meadows. In addition to *M. pennsylvanicus* and *C. gapperi*, other species trapped in association with long-tailed voles are *Peromyscus maniculatus*, *Eutamias minimus*, *Zapus hudsonius*, and *Sorex cinereus*.

Reproductive data for long-tailed voles in the Black Hills are adequate only for July. Of two females taken west of Hill City in mid-June 1965, one carried five embryos which were 10 in crown-rump length; the other showed no signs of reproductive activity. Testicular length of a male obtained on 28 June 1967 was 12. Fifteen of 23 females captured in July were pregnant; there was an average of 4.7 (4-6) embryos in each, which were 10.3 (3-24) in crown-rump length. One female collected northwest of Deerfield on 8 July 1965 had eight placental scars; another taken east of Buckhorn on 18 July 1951 was lactating. An additional female trapped southwest of Lead on 30 July 1968 had a swollen uterus, possibly indicating recent implantation. Testes of 12 adult males captured in July had an average length of 11.2 (10-12). On 9 August 1967, two females were captured south of Spearfish; one carried six embryos that were 4 in crown-rump length, whereas the other was lactating and had seven placental scars. Juvenile and subadult long-tailed voles are common in collections made throughout July and August, and many of the pregnant females were subadults.

Five young voles taken in Beaver Creek Valley in early July were in juvenal pelage, which was fine, soft, and dark. Twelve juveniles collected throughout July either had completed post-juvenal molt, or replacement of juvenal pelage was in process with new hairs exposed beneath the old pelage on the sides and dorsum. In the same period, three subadults were molting to an adult pelage. In adults, change from old, faded winter pelage to fresh summer pelage was noted in late June and early July; irregular patches of new hair occurred on the rump and over the shoulders.

A male trapped in Beaver Creek

Valley on 8 July 1965 harbored ticks of the *Ixodes ochotonae-angustus* complex.

Significant secondary sexual dimorphism was not evident in comparison of 14 adult males with 17 adult females from the Black Hills, although males are slightly larger in most measurements and females (50.9±0.25) reflect reds more intensely than males (48.8±0.15). A distinct pattern of variation in coloration or size within the Hills populations is not discernible.

Bailey (1900:48) noted that *M. l. longicaudus* and *M. l. mordax* are "very similar" in external and cranial dimensions. After examining specimens from Idaho and throughout Wyoming, Long (1965:655) placed *mordax* in the synonomy of *longicaudus*, pointing out that C. H. Merriam selected an atypically dark vole with long ears as the holotype. When 31 long-tailed voles from the Hills were compared with 29 from north-central Wyoming (Big Horn, Fremont, Johnson, Sheridan, and Washakie counties) and 80 from southeastern Wyoming (Albany, Carbon, Converse, Laramie, and Natrona counties); the former averaged darker in tone and possessed longer ears and maxillary tooth-rows (Table 24).

Even though the pelage of *M. longicaudus* is extremely uniform in reflectance of various hues, this species is quite variable throughout its range in all other parameters. For example, relative to the Black Hills population, 28 individuals from Carbon County, Wyoming, are darker in tone of color (21.0±1.98), 17 specimens from Natrona County have a similar average length of ear (15.8± 1.59), and single representatives from Washakie and Sheridan counties each have longer maxillary tooth-rows (7.5 and 7.0, respectively). Thus, the above-mentioned apparent differences attributable to the Black Hills population of *M. longicaudus* easily fall within the range of variation of populations southward and westward of the Hills, and I must concur with the findings of Long (*loc. cit.*). Average color and cranial measurements additional to those given in Table 24 for 31 adults from the Black Hills are: percent red reflectance, 50.0±0.23; percent green reflectance, 26.7±0.18; percent blue reflectance, 23.3±0.16; weight, 41.9±7.04; interorbital constriction, 3.8±0.15; length of incisive foramen, 5.0±0.23.

Specimens examined (172).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 3 mi S Spearfish, 4200 ft, 2; Tinton, 5900 ft, 1; 2 mi S Tinton, 6100 ft, 4; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 3; Cheyenne Crossing, 8 mi SW Lead, 1 (SDSU); Boxelder Creek, Steamboat Rock Campgrounds 1 (NRW); Dumont, 1 (USNM). *Meade County:* 7 mi S, 1 mi W Sturgis, 4700 ft, 1. *Pennington County:* Rapid Creek, 1.5 mi W Rochford, 4 (UMMZ); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 17; Ditch Creek, 14 mi W Hill City, 6400 ft, 2; Redfern, 1 (USNM); 20 mi N Elk Mountain, 6000 ft, 12; 17 mi NW Custer, 7 (UMMZ); 16 mi NW Custer, 23 (UMMZ); Palmer Gulch, 3 mi SE Hill City, 5300-5400 ft, 7 (UMMZ); Nelson's Place, 4 mi SE Hill City, 5300-5400 ft, 2 (UMMZ); Palmer Gulch, 5 mi SE Hill City, 2 (UMMZ); unspecified locality, 5 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 4 (FMNH); 16 mi W Custer, 7 (USNM); Custer, 6 (2 USNM, 4 AMNH); 4 mi E Custer, Harney National Forest, 1 (UMMZ); Elk Mountain, 4900 ft, 4 (USNM); 4 mi SW Custer, 1; 18 mi SW Custer, 5300 ft, 5 (USNM); Bull Springs, 2 mi N, 9 mi W Custer, 8 (UMMZ).

WYOMING: *Crook County:* Bear Lodge Mountains, Warren Peak, 6000 ft, 1 (USNM); Bear Lodge Mountains, 6.5 mi SSE Alva, 1 (UMMZ); 3 mi NW Sundance, 5900 ft, 7; 1.5 mi NW Sundance, 5000 ft, 1; Sundance, 6000 ft, 12 (USNM); Rattlesnake Creek, 6000 ft, 2 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 15; 4 mi E Four Corners, 1.

Additional record.—SOUTH DAKOTA: *Pennington County:* Rochford (BB).

Microtus ochrogaster haydenii (Baird)

Prairie Vole

Arvicola (Pedomys) haydenii Baird, 1858, *in* Reports of explorations and surveys . . . from the Mississippi River to the Pacific Ocean . . ., 8(1):543, 14 July (type locality, Fort Pierre, Stanley Co., South Dakota).

Microtus ochrogaster haydenii—Osgood, 1907, Proc. Biol. Soc. Washington, 20:48, 18 April.

Microtus ochrogaster, in contrast to

TABLE 24.—Geographic variation in selected color, and external and cranial measurements of adult *Microtus longicaudus* from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Total length	Tail length	Hind foot length	Ear length	Greatest length of skull	Zygomatic breadth	Lambdoidal breadth	Rostral length	Length of maxillary tooth-row	Skull depth
31 (14♂, 17♀)					Black Hills, South Dakota and Wyoming						
Mean	21.7	178.9	59.3	21.3	15.8	27.3	15.0	12.4	8.7	6.8	10.5
SD	±2.82	±8.97	±4.45	±0.80	±1.48	±0.87	±2.05	±0.51	±0.42	±0.27	±0.35
29 (18♂, 11♀)					North-central Wyoming						
Mean	25.1	176.6	57.4	21.3	14.4	27.6	15.2	12.5	8.8	6.7	10.6
SD	±2.94	±8.02	±6.28	±0.75	±1.40	±0.95	±0.81	±0.56	±0.38	±0.22	±0.36
80 (49♂, 31♀)					Southeastern Wyoming						
Mean	22.7	176.5	59.2	20.6	14.4	27.2	15.0	12.2	8.6	6.6	10.4
SD	±2.71	±8.39	±5.07	±1.20	±1.76	±0.71	±0.59	±0.46	±0.37	±0.29	±0.35

other members of the genus that occur in the study area, is relatively tolerant of xeric conditions and is widely distributed wherever suitable grassy habitats are available on the Great Plains of central North America. Prairie voles have been taken in all counties within the Black Hills, and are found in the drier valley systems that penetrate the foothill transition zone. They occur up to 5000 feet, but are most abundant below 4400 feet along the interface of the surrounding prairie. Wasteland, dry ditches along roadways, and lightly grazed pastures also are inhabited by this vole. Vernon Bailey (1888:445) reported the first specimens of *M. ochrogaster* in the Black Hills region.

From 7 to 11 August 1967, a survey was taken along the floor of Big Spearfish Canyon, out onto the adjacent prairie. The vegetation of this moist northern canyon system is rather diverse. At higher elevations, ponderosa pine is fairly restricted to the arid bluffs and white spruce dominates the mesic canyon bottoms, along with rushes, sedges, dense stands of tall grasses, deciduous shrubs, and quaking aspen; *Clethrionomys gapperi, Microtus longicaudus*, and *M. pennsylvanicus* were taken in these areas. Descending along the canyon, conditions gradually became less mesic. Deciduous elements such as bur oak, willow, paper birch, quaking aspen, boxelder, bunchberry, and alder are abundant. The understory of parklike woodlands and small meadows is composed of wild gooseberry (*Ribes missouriense*), wild strawberry (*Fragaria virginiana*), chokecherry, poison ivy, solomon's seal, starry solomonplume (*Smilacina stellata*), yellow lady's slipper (*Cypripedium* sp.), white geranium (*Geranium bicknellii*), black-eyed susan, sunflower, burdock (*Arctium minus*), cinquefoil (*Potentilla* sp.), and meadow sweet (*Spiraea lucida*). Along Spearfish Creek, and adjacent moist areas at these intermediate elevations are snowberry, horsetail (*Equisetum* sp.) flowering fern (*Osmunda* sp.), wood fern (*Dryopteris* sp.), rushes, and sedges; *Microtus longicaudus* and *M. pennsylvanicus* were obtained in these areas, but *Cleithrionomys* no longer was taken. Below 4000 feet, upward extensions of the xeric prairie were encountered as evidenced by the presence of thistles, soapweed, mustards, and an occasional pricklypear cactus. Prairie voles were taken under these conditions, whereas the other three microtines were no longer encountered.

Fifty-eight individuals were captured southwest of Minnekahta (13-18 June 1967) on slopes that form the southern limits of the Black Hills. The area consists of arid grassy pastureland, expanses of dryland farming (mostly small grains), and a series of ridges upon which ponderosa pine and western red cedar grow. Most of the voles were taken along fencerows bordering agricultural fields, in vegetation composed of bluegrass, brome grass, cord grass, western wheat grass, and scattered forbs. Vole runways were well-defined but localized, and piles of grass cuttings were common. Specimens collected near Hot Springs were on grass ridges and in apple orchards that flank the Fall River.

Wind Cave National Park extends through the gently rolling foothills of the transition zone, grading into the more rugged topography of the southeastern portion of the Black Hills. Here, where *M. ochrogaster* is one of the commonest small mammals, the mixed-grass prairie of the plains intermingles with the ponderosa pine of the higher elevations. Chokecherry, wild plum (*Prunus americana*), wild rose, hackberry, and sagebrush are interspersed with prairie grasses and forbs. Other mammals trapped in the runways of this species were *Peromyscus maniculatus, Perognathus hispidus, Mus musculus*, and *Reithrodontomys megalotis*.

Reproductive activity was substantial from late spring throughout the summer, and continued at least into early autumn. Three females captured in late March and early April carried 4.3 (4-5) embryos that had an average crown-rump

length of 5.7 (2-10). Reproductive data are unavailable for May, early June, and July (except for one female captured on 26 July 1968 that carried three embryos which were 8 in crown-rump length). Field work during these periods was undertaken at higher elevations where prairie voles do not occur, thus explaining the lack of data. Sixteen of 26 females taken in the last half of June were pregnant, containing 3.5 (1-6) embryos that had an average crown-rump length of 10.5 (3-20). Two other females had 3.0 (2-4) placental scars, and another female had an enlarged uterus, which possibly indicates recent implantation. Average testicular length of 22 adult males obtained in this period was 11.0 (7-17). In the latter part of August, three of nine females examined contained fetuses. The average number of fetuses was 3.7 (3-4); the average crown-rump length of the fetuses was 11.3 (6-20). Two other females had five placental scars each. The average length of the testes of 11 males obtained in August was 13.0 (10-18). Five of eight females captured in early September were pregnant, and contained an average of 3.8 (3-5) embryos that were 15.2 (8-22) in crown-rump length; four placental scars were manifest in the reproductive tract of one other female. The average testicular length of five adult males obtained about this time was 12.6 (9-17). Juveniles and subadults are common in collections made from April through September; several of the gravid females were nearly mature subadults.

Due to the high reproductive rate of this species, seasonal aspects of molt were difficult to discern. Juveniles were in a fine dark pelage, although many were commencing the post-juvenal molt. As voles attained about three-quarters of adult size and adult pelage replaced that of the subadults, new hairs could be observed underlying the older fur on the dorsum and sides, and occasionally on the venter. Irregular patches of molt were noted on adults in all months from which specimens were examined. Pelage replacement in adults seems to be more erratic than in subadults and possibly extends over a greater period of time.

Prairie voles from the Hills are heavily infested with various types of ectoparasites as follow: a louse, *Hoplopleura acanthopus* (Burmeister); a tick, *Ixodes spinipalpis* Hadwen and Nuttall; two fleas, *Orchopeas leucopus* (Baker), and *Monopsyllus wagneri* (Baker); two chiggers, *Eutrombicula alfreddugesi* (Oudemans), and *Euschoengastia setosa* (Ewing); and seven mites, *Dermacarus hypudaei* (Koch), *Mycoptes musculinus* (Koch), *Haemolaelaps fahrenholzi* Berlese, *Androlaelaps fahrenholzi* (Berlese), *Laelaps microti* (Ewing), *Ornithonyssus bacoti* (Hirst), and *Haemogamasus ambulans* (Thorell).

Examination of 26 adult male and 23 adult female *M. ochrogaster* from the Black Hills revealed no secondary sexual differences in coloration, external measurements or most cranial dimensions. However, females (6.9±0.32) are significantly greater than males (6.6±0.29) in length of maxillary tooth-row. A pattern of variation within the Hills was not evident. When comparisons were made with populations from other areas in South Dakota and Wyoming, the great variability of *M. ochrogaster* became apparent (Tables 25 and 26). Characters seem to vary independently and no definite trends are discernible, although specimens from the Hills tend to be darker in tone of color and relatively large in external and cranial dimensions. Measurements additional to those given in Table 26 for 44 adult prairie voles from the Hills are: hind foot length, 20.2±0.94; lambdoidal breadth, 12.4±0.39; interorbital constriction, 4.0±0.13; length of incisive foramen, 5.0±0.32; and length of maxillary tooth-row, 6.7±0.34.

Specimens examined (214).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 1.5 mi S, 0.5 mi E Spearfish, 3800 ft, 6. *Meade County:* Black Hawk, 22 (AMNH). *Pennington County:* 8 mi NE Rapid City, 4 (UMMZ); 4 mi N Rapid City, 2 (AMNH); South Canyon, 3 mi W Rapid City, 13 (6 AMNH, 7 NRW); Rapid City, 9 (4 USNM,

TABLE 25.—Geographic variation in coloration of the mid-dorsal pelage of adult *Microtus ochrogaster* obtained in summer from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Percent red reflectance	Percent green reflectance	Percent blue reflectance
41 (22♂, 19♀)		Black Hills, South Dakota and Wyoming		
Mean	20.0	48.0	27.5	24.5
SD	±2.97	±0.20	±0.18	±0.16
20 (11♂, 9♀)		Harding County, South Dakota		
Mean	21.8	48.1	27.3	24.6
SD	±3.00	±0.26	±0.18	±0.15
8 (4♂, 4♀)		Bennett County, South Dakota		
Mean	23.6	47.6	26.8	25.6
SD	±4.72	±0.28	±0.21	±0.13
4 (2♂, 2♀)		Campbell County, Wyoming		
Mean	19.9	52.7	24.6	22.7
SD	±1.84	±0.24	±0.13	±0.20
2 (1♂, 1♀)		Weston County, Wyoming		
Mean	25.5	46.1	28.5	25.4
SD	±2.12	±0.03	±0.10	±0.06
5 (4♂, 1♀)		Converse County, Wyoming		
Mean	21.2	48.1	27.4	24.5
SD	±2.41	±0.42	±0.38	±0.08
16 (8♂, 8♀)		Niobrara County, Wyoming		
Mean	23.2	51.3	25.7	23.0
SD	±3.12	±0.33	±0.23	±0.16

5 NRW); 1 mi SW Rapid City, 2 (UMMZ); West Dark Canyon, 1 mi S, 4 mi W Rapid City, 2 (AMNH); near Rim Rock, 2 (AMNH); Bald Hills, south Pactola, 4 (USNM); Spring Creek, 4 mi ENE Rockerville, 3600 ft, 7 (UMMZ); Spring Creek, south Rapid City, 10 (8 AMNH, 2 MHM); unspecified locality, 1 (SDMT). *Custer County:* Beaver Creek, 3 mi NW Wind Cave National Park, 1 (UW); Wind Cave National Park, 9 (7 UMMZ, 2 WCNP); 6 mi N, 1 mi E Wind Cave, Wind Cave National Park, 4400 ft, 1; 2.5 mi N, 5 mi E Wind Cave, Wind Cave National Park, 3700 ft, 5; 1.5 mi N, 1.5 mi W Wind Cave, Wind Cave National Park, 3250 ft, 4; Buffalo Corral, Wind Cave National Yark, 4300 ft, 1; Headquarters, Wind Cave National Park, 4100 ft, 8; Housing Area, Wind Cave National Park, 4100 ft, 2; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 3; Elk Mountain, 4800 ft, 3 (USNM); unspecified locality, 9 (UMMZ). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 58; 1 mi N, 5.5 mi E Hot Springs, 3400 ft, 4; 1 mi N, 6 mi E Hot Springs, 3400 ft, 11; 4 mi E Hot Springs, 3400 ft, 3; Hot Springs, 1 (UW); 2 mi S, 2 mi E Hot Springs, 3600 ft, 1.

WYOMING: *Crook County:* 15 mi NE Sundance, 3825 ft, 1; 1.5 mi NW Sundance, 5000 ft, 1; Sundance, 2 (USNM); Sand Creek, 3750 ft, 1 (USNM). *Weston County:* 1 mi N Newcastle, 4800 ft, 1 (UMMZ); Newcastle, 1 (USNM).

Additional record.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB).

Microtus pennsylvanicus insperatus (J. A. Allen)

MEADOW VOLE

Arvicola insperatus J. A. Allen, 1894, Bull. Amer. Mus. Nat. Hist., 6:347, 7 December (type locality, Custer, Custer Co., South Dakota).

Microtus pennsylvanicus insperatus—Anderson, 1943, Canadian Field-Nat., 57:92, 17 October.

The meadow vole occupies streamside habitats and mesic areas adjacent to reservoirs and other impoundments throughout the Northern Great Plains.

TABLE 26.—Geographic variation in selected external and cranial measurements of adult *Microtus ochrogaster* from the Northern Great Plains.

Number and sex of specimens averaged	Total length	Tail Length	Ear length	Weight	Greatest length of skull	Zygomatic breadth	Rostral length	Skull depth
44 (24♂, 20♀)			Black Hills, South Dakota and Wyoming					
Mean	158.1	37.5	13.7	48.5	27.9	16.1	9.0	11.0
SD	±9.86	±3.47	±1.66	±6.37	±1.06	±0.69	±0.51	±0.34
20 (11♂, 9♀)			Harding County, South Dakota					
Mean	158.8	36.2	13.1	46.7	27.9	15.7	8.9	10.9
SD	±9.39	±4.19	±1.98	±4.68	±1.06	±0.67	±0.42	±0.32
8 (4♂, 4♀)			Bennett County, South Dakota					
Mean	152.2	34.2	11.7	36.0	27.2	15.1	8.8	10.7
SD	±8.38	±4.83	±1.03	±2.88	±0.88	±0.39	±0.26	±0.47
4 (2♂, 2♀)			Campbell County, Wyoming					
Mean	145.7	34.7	14.2	37.2	26.8	15.2	8.2	10.5
SD	±3.86	±4.99	±2.06	±4.03	±0.82	±0.47	±0.37	±0.41
2 (1♂, 1♀)			Weston County, Wyoming					
Mean	171.5	41.0	13.0	49.5	28.8	16.3	9.3	11.3
SD	±7.78	±0.00	±0.00	±7.99	±1.20	±1.38	±0.71	±0.32
5 (4♂, 1♀)			Converse County, Wyoming					
Mean	160.8	40.2	14.8	47.7	28.3	15.8	8.9	11.0
SD	±4.21	±4.27	±1.64	±3.59	±1.01	±0.64	±0.44	±0.24
16 (8♂, 8♀)			Niobrara County, Wyoming					
Mean	167.1	39.7	14.1	47.3	28.1	16.2	9.0	11.1
SD	±9.71	±4.57	±1.54	±6.74	±1.27	±0.89	±0.47	±0.50

Altitudinal range within the Black Hills is from 3700 to 6500 feet, but the species is most common above 5000 feet. Range of tolerance of environmental conditions seems to be greater in *Microtus pennsylvanicus* than in any other microtine from the study area. Meadow voles occur from the mesic boreal cap of the Hills, down through the semiarid foothill transition zone, and onto the arid plains in suitable riparian habitats; they are active in all seasons. Although this microtine is the commonest member of the genus in the Black Hills, specimens are lacking from Meade and Fall River counties.

Streamside habitats in canyons of spruce, aspen, willows, sedges, grasses, rushes, deciduous bushes and scattered forbs are favored by this species at higher elevations; 52 meadow voles (19 males and 33 females) were taken south of Tinton under these general conditions in mid-July 1961. Swampy lowlands, borders of beaver ponds and cattail (*Typha* sp.) marshes, and moist meadows of bluegrass, spearmint (*Mentha spicata*), stinging nettle (*Urtica* sp.), red clover (*Trifolium pratense*), and assorted forbs are occupied at lower elevations. Individuals captured northeast of Sundance (early July 1947), west of Nemo (late June 1947) and in Wind Cave National Park (summer 1968) are from such environs. Traps placed among mossy rocks and ferns under overhanging stream banks throughout the Hills also proved to be productive in capturing meadow voles.

Due to its wide ecological distribution, *Microtus pennsylvanicus* is syntopic with three other species of voles in the Black Hills region. Association of this species with *Microtus longicaudus* already has been discussed (see account

of that species). Morris (1969:299) reported an almost complete habitat separation between *M. pennsylvanicus* and *Clethrionomys gapperi* in Saskatchewan, with the former being confined to grassland and the latter to aspen woodland. In the Hills, however, both species frequently were taken in the same habitat. Although *M. pennsylvanicus* was not captured in stands of aspen or other woodlands, *C. gapperi* often was obtained in grassland and riparian situations where brush, woodpiles, and fallen logs were common; here, the two species occurred side by side. At lower elevations, where the meadow vole and prairie vole occur together. *M. pennsylvanicus* inhabits the lower, wetter areas and *M. ochrogaster* the drier places. For example, in Wind Cave National Park, the meadow vole occupies the immediate brushy banks of Beaver Creek, whereas the prairie vole occupies the grassy upland adjacent to the creek. In addition to the above named species, *Peromyscus maniculatus, Eutamias minimus, Zapus hudsonius,* and *Sorex cinereus* were taken in the same traplines with *M. pennsylvanicus.*

Reproductive data for meadow voles in the Black Hills are available only for the period from mid-June through early August. Bailey (1924:528) indicated that parturient female *M. pennsylvanicus* have been taken in all seasons. Four of six females captured in late June carried 5.8 (5-7) embryos that had an average crown-rump length of 17.3 (7-27). One other individual had six placental scars. The average testicular length of 17 adult males obtained in June was 12.8 (10-15). Thirty-four of 50 females captured in July were pregnant; the average number of embryos was 5.9 (2-9), and their average length was 12.1 (4-27). Four other females were lactating and another four had enlarged uteri, possibly denoting recent implantation. The average length of testes of 23 males obtained in July was 14.4 (10-18). A female captured north of Sundance on 15 August 1951 carried six fetuses and another obtained southwest of Rapid City on 25 August 1952 contained eight (21 in crown-rump length). A subadult female taken in Wind Cave National Park on 1 September 1968 was gravid, carrying three embryos that were 27 in crown-rump length. Many of the other above-mentioned pregnant females were nearly mature subadults. Juveniles are common in collections made from June through August, and undoubtedly in other periods as well.

The process of pelage replacement in *M. pennsylvanicus* is similar to that described for other microtines in the Black Hills. Adults molt from pale, faded winter pelage to fresh, dark summer pelage in late June and July. All stages of molt, from commencement to completion, can be observed in adults taken on the same day at the same locality in mid-summer. Juveniles were in a fine, dark fur that was replaced by subadult pelage. Developmental pelage replacement depends on chronology and rate of maturation of the individual; thus, concurrent existence of several different-aged litters tends to complicate interpretation of precise seasonal aspects of molt.

In the Black Hills, *M. pennsylvanicus* are parasitized externally by ticks, *Dermacentor andersoni* Stiles, *Ixodes spinipalpis* Hadwen and Nuttall, and members of the *Ixodes ochotonae-angustae* complex, by laelaptid mites, *Laelaps microti* (Ewing) and *Androlaelaps fahrenholzi* (Berlese), and by a chigger, *Euschoengastia setosa* (Ewing).

J. A. Allen (1877:176) first reported meadow voles from the Black Hills area under the name *Arvicola riparius,* and later (1894b:347) assigned Hills specimens to a new subspecies, *insperatus.* In his revision of the genus *Microtus,* V. Bailey (1900:20) listed *Arvicola insperatus* in the synonomy of *M. p. modestus,* but later (1920:72) included Black Hills specimens under the name *M. p. wahema* described from eastern Montana and western North Dakota: R. M. Anderson (1943:92) returned *insperatus* to subspecific rank, concluding

that *wahema* was not distinct. S. Anderson (1956) discussed subspeciation in the meadow vole in the western part of its range.

Examination of 31 adult male and 37 adult female *M. pennsylvanicus* from the Black Hills revealed no secondary sexual variation in coloration. Males are significantly larger than females in lambdoidal breadth (12.3±0.46, 11.9±0.37) and length of incisive foramen (5.5± 0.31, 5.3±0.20), and are slightly larger in most other dimensions. A pattern of variation in external and cranial dimensions is not discernible within the Hills but four specimens from west of Nemo (15.0±1.78) and six from northeast of Custer (15.1±1.28) are darker in tone of color on the average than 14 individuals from east of Buckhorn (18.6±1.42), five from northeast of Sundance (18.3± 2.17), 27 from south of Tinton (17.3± 1.87) and six from Beaver Creek Valley (16.5±1.18).

Microtus pennsylvanicus insperatus is evidently quite variable throughout its geographic range in external and cranial dimensions, but each character seems to vary independently and no trends are apparent (Table 27). Meadow voles from the Black Hills are much darker in comparison to specimens from Wyoming and Montana, but voles from Harding County, South Dakota, approach the color of those of the Hills in tone. Measurements additional to those in Table 27 for 68 adult *M. pennsylvanicus* from the Black Hills are: percent red reflectance, 51.2±0.24; percent green reflectance, 25.9±0.20; percent blue reflectance, 22.6±0.24; hind foot length, 20.8 ±3.83; weight, 48.6±7.44; interorbital constriction, 3.6±0.15; length of incisive foramen, 5.4±0.27; and length of maxillary tooth-row, 6.7±0.21.

Specimens examined (301).—SOUTH DAKOTA: *Lawrence County:* Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 4;

TABLE 27.—Geographic variation in selected color, and external and cranial measurements of adult *Microtus pennsylvanicus* from the Northern Great Plains.

Number and sex of specimens averaged	Tone of color	Total length	Tail length	Ear length	Greatest length of skull	Zygomatic breadth	Lambdoidal breadth	Rostral length	Skull depth
68 (31♂, 37♀)				Black Hills, South Dakota and Wyoming					
Mean	17.2	164.8	41.7	13.5	27.6	15.1	12.0	8.4	10.7
SD	±2.00	±6.30	±3.61	±1.42	±0.79	±0.52	±0.45	±0.38	±0.32
5 (2♂, 3♀)				Harding County, South Dakota					
Mean	17.5	164.4	43.0	12.8	27.4	15.6	12.3	8.3	10.6
SD	±2.00	±9.71	±4.06	±1.30	±1.11	±0.41	±0.27	±0.54	±0.24
7 (4♂, 3♀)				Campbell County, Wyoming					
Mean	19.1	172.1	44.3	13.4	27.5	14.8	11.5	8.6	10.8
SD	±2.65	±4.02	±2.75	±2.30	±0.81	±0.50	±0.70	±0.41	±0.22
29 (16♂, 13♀)				Johnson County, Wyoming					
Mean	19.3	168.3	49.1	13.0	27.4	15.5	12.2	8.3	10.8
SD	±2.32	±7.97	±2.98	±0.74	±0.57	±0.66	±0.39	±0.30	±0.39
16 (7♂, 9♀)				Sheridan County, Wyoming					
Mean	19.9	169.3	44.3	13.9	27.9	15.4	12.4	8.3	11.0
SD	±1.41	±8.27	±4.22	±0.81	±0.62	±0.54	±0.34	±0.26	±0.40
10 (4♂, 6♀)				Philips County, Montana					
Mean	19.8	162.5	49.3	12.3	26.9	14.7	11.8	8.0	10.6
SD	±2.08	±4.35	±2.11	±0.67	±0.56	±0.36	±0.28	±0.31	±0.26

2 mi S Tinton, 6100 ft, 52; Roubiax Lake, 2 (NRW); 2 mi W Nemo, 4700 ft, 6. *Pennington County:* Rapid City, 1 (NRW); Rapid Creek, 1.5 mi W Rochford, 3 (UMMZ); 2 mi W Oreville, 5500 ft, 1 (UMMZ); Beaver Creek, 4 mi N, 10.5 mi W Deerfield, 6400 ft. 18; Beaver Creek, 3 mi N, 9 mi W Deerfield, 6400 ft, 6; Castle Creek, 6500 ft, 7 (UMMZ); Bald Hills, Pactola, 3 (USNM); 6 mi S, 9.5 mi W Rapid City, 3; Sheridan Lake, 2 (NRW); Spring Creek, south Rapid City, 1 (MHM); 4 mi NW Hill City, 2 (UMMZ); 20 mi N Elk Mountain, 6000 ft, 5 (USNM); Moon, 22 mi W Hill City, 6200 ft, 7; Ditch Creek, 14 mi W Hill City, 6400 ft, 1; Hill City, 1 (AMNH); near Palmer Gulch, 1 (UMMZ); Palmer Gulch, 3 mi SE Hill City, 5300-5400 ft, 25 (UMMZ); Nelson's Place, 4 mi SE Hill City, 5300-5400 ft, 10 (UMMZ); 16 mi NW Custer, 3 (UMMZ); Horse Thief Lake, near Mount Rushmore, 1 (NRW); unspecified locality, 3 (UMMZ). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 14 (FMNH); 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 12; 0.5 mi E Sylvan Lake, 6250 ft, 1 (UMMZ); 5.75 mi N 5.75 mi E Custer, 5220 ft, 13; Custer, 5 (AMNH); Harney National Forest, 4 mi E Custer, 2 (UMMZ); 3 mi N Pringle, 5000 ft, 3 (UMMZ); Lightning Creek, 8 mi SW Custer, 5100 ft, 1 (UMMZ); Beaver Creek Canyon, Wind Cave National Park, 4200 ft, 8; Headquarters, Wind Cave National Park, 4100 ft, 1; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 1; Bull Springs, 2 mi N, 9 mi W Custer, 9 (UMMZ).

WYOMING: *Crook County:* Bear Lodge Mountains, 2 (USNM); Bear Lodge Mountains, 6.5 mi SSE Alva, 2 (UMMZ); 15 mi N Sundance, 5500 ft, 3; 15 mi ENE Sundance, 3825 ft, 6; 3 mi NW Sundance, 5900 ft, 1; 1.5 mi NW Sundance, 5000 ft, 4; Sundance, 15 (USNM); Rattlesnake Creek, 6000 ft, 1 (USNM); Sand Creek, 3750 ft, 2 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 25; Newcastle, 2 (USNM).

Additional records.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB). *Pennington County:* (BB). *Custer County:* French Creek, 3 mi E Custer (Stebler, 1939:390).

Ondatra zibethicus cinnamominus (Hollister)

Muskrat

Fiber zibethicus cinnamominus Hollister, 1910, Proc. Biol. Soc. Washington, 23:125, 2 September (type locality, Wakeeney, Trego Co., Kansas).

Ondatra zibethicus cinnamomina—Miller, 1912, Bull. U. S. Nat. Mus., 79:232, 31 December.

The muskrat is characteristic of the prairie sloughs, marshes, and drainage systems of the Northern Great Plains and is common on nearly all streams that originate in the Black Hills. Although few specimens of this semiaquatic microtine are available, I have observed muskrats throughout the Hills. Dens and submerged trailways interlace the shorelines of lakes and reservoirs, and penetrate banks of all water courses of the region. In the past, *Ondatra* undoubtedly has been one of the most commercially important fur-bearers sought by trappers in the Black Hills, but more recently, muskrat pelts have fetched relatively poor prices. Burrows excavated in dams and irrigation ditches cause extensive damage to these structures and lend a negative dimension to the economic importance of this species.

Compared to *O. z. osoyoosensis* to the west in Wyoming, *O. z. cinnamominus* is smaller cranially, with a notably shorter maxillary tooth-row, and is paler in color, being more reddish or buffy instead of brownish (Long, 1965:662). The species was first reported from the Black Hills by Bailey (1888:445).

Reproductive and natural history data are lacking for this microtine in western South Dakota, but in northern Nebraska, the muskrat breeds from late April to early September—adult females produce one to four litters per year, averaging about six young per litter (Jones, 1964: 235).

Specimens examined (24).—SOUTH DAKOTA: *Lawrence County:* Little Spearfish Canyon, Savoy, 4 (USNM). *Pennington County:* Rapid City, 2 (1 USNM); Diamond S Ranch, near Rapid City, 2 (UMMZ); Spring Creek, south of Rapid City, 2 (MHM); Tigerville, near Hill City, 1 (USNM); Hill City, 3 (AMNH); Harney National Forest, 1 (UMMZ). *Custer County:* Custer, 8 (7 AMNH, 1 FMNH). *Fall River County:* 1 mi N Hot Springs, 1 (UW).

Additional records.—SOUTH DAKOTA: *Custer County:* French Creek, 3 mi E Custer (Stebler, 1939:390). *Fall River County:* Hot Springs (Woodward, 1930:109).

Family MURIDAE—Old World Rats and Mice

The two species of murids occurring in the Black Hills are commensals of man,

and were introduced into North America from the Old World in the mid-eighteenth century.

Rattus norvegicus (Berkenhout)

Norway Rat

Mus norvegicus Berkenhout, 1769, Outlines of the natural history of Great Britain and Ireland, 1:5 (type locality, England, where the species was introduced from Asia, probably via Continental Europe, in the early 1700's).

Rattus norvegicus—Hollister, 1916, Proc. Biol. Soc. Washington, 29:126, 6 June.

The Norway rat was introduced to the colonies of eastern United States from the Old World about 1775, escaping from ships at various seaports (Silver, 1941: 2). I do not know the history of its immigration into the Black Hills region, but the species presumably was introduced at river towns and forts along the Missouri Valley in the 1850's and subsequently dispersed in a manner similar to *Mus musculus*, as described in the following account.

I know of only two actual specimens from the study area, but Over and Churchill (1945:45) indicated that these rats were found occasionally in the Black Hills, in and around habitations of man.

Specimens examined (2).—SOUTH DAKOTA: *Pennington County:* Rapid City, 2 (SDMT).

Additional record.—SOUTH DAKOTA: "Black Hills" (Over and Churchill, 1945:45).

Mus musculus Linnaeus

House Mouse

[*Mus*] *musculus* Linnaeus, 1758, Systema naturae, ed. 10, 1:62 (type locality restricted to Upsala, Sweden, by Thomas, Proc. Zool. Soc. London, p. 147, March 1911).

The house mouse is a common, often abundant, rodent that frequently is injurious to man and to the native fauna. It resides in and around human habitations at lower elevations in the Black Hills. For example, on 13 June 1967, several dozen individuals were killed with .22 dust-shot in grain bins near Minnekahta, Fall River County. Wild populations occasionally are encountered.

This rodent was introduced from Europe in early times and has since spread over most of temperate and tropical North America. I am unfamiliar with the history of its dispersal to the Black Hills, but *Mus musculus* presumably was introduced in the plains area throughout the Mississippi and Missouri river valleys from river boats to wharves of forts and trading posts; thence, it probably spread into the study area in company with early military expeditions and the establishment of settlements. Hayden (1859:710) mentioned that both the house mouse and Norway rat were abundant at all of the fur trading posts on the Missouri River in the 1850's.

Because two subspecific stocks were introduced into North America (Schwarz and Schwarz, 1943:65), I choose not to assign a subspecific identity to specimens from the Black Hills.

A female taken southeast of Spearfish in mid-August evidenced six placental scars, whereas another obtained in Wind Cave National Park in late August showed no signs of reproductive activity. Testicular lengths of two males obtained in June from near Minnekahta were 5.

Specimens examined (25).—SOUTH DAKOTA: *Lawrence County:* 1.5 mi S, 0.5 mi E Spearfish, 3800 ft, 1; 8 mi SW Lead, 1 (UW). *Meade County:* Black Hawk, 1 (AMNH). *Pennington County:* 4 mi N Rapid City, 3 (AMNH); Rapid City, 12 (10 NRW, 2 SDMT); Glendale, 1 (AMNH). *Custer County:* Squaw [Grace Coolidge] Creek, 1 (AMNH); 2.5 mi N, 5 mi E Wind Cave, Wind Cave National Park, 3700 ft, 1; Wind Cave Canyon, Wind Cave National Park, 4100 ft, 1; Wind Cave National Park, 1 (USNM). *Fall River County:* 0.5 mi S, 1.5 mi W Minnekahta, 4200 ft, 2.

Additional record.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB).

Family ZAPODIDAE—Jumping Mice

Zapodids, represented in the Black Hills region by one species, are saltatorial rodents that abide in areas of lush vegetation such as wet meadows or streamside communities. Aridity is the major factor restricting the distribution of jumping mice on the Northern Great Plains.

Zapus hudsonius campestris Preble

MEADOW JUMPING MOUSE

Zapus hudsonius campestris Preble, 1899, N. Amer. Fauna, 15:20, 8 August (type locality, Bear Lodge Mountains, Crook Co., Wyoming).

Although specimens are absent from Meade and Fall River counties, the meadow jumping mouse is common throughout the study area. It most frequently occurs in riparian communities along small streams in valley meadows, or in open, moist habitats within coniferous forests that support a low undergrowth of forbs and grasses. *Zapus hudsonius* occurs in suitable habitats on the adjacent plains, but is most frequent in the Black Hills up to 6500 feet. This species hibernates in winter, and all specimens at hand were taken in warmer months; earliest and latest seasonal records are 4 June and 27 August, respectively.

Jumping mice collected in this study were trapped along drainage systems, in dense grasses and sedges that were interspersed with deciduous shrubs and fallen logs of aspen, birch, willow, white spruce, and ponderosa pine. Most of the specimens from the Wyoming part of the Hills, and those individuals from Little Spearfish, Big Spearfish, and Beaver Creek canyons were taken under these general conditions. Similarly, five females and three males were trapped in a large valley of approximately one mile in length located southwest of Keystone. A stream, with many small tributaries, flowed through the center of the valley and created a semimarsh situation. Lush vegetation was mainly of tall grasses and some very dense patches of clover; deciduous shrubs bordered the stream.

Forty-two individuals (22 males and 20 females) were taken in the lowland habitat of Grizzly and Iron creeks, northeast of Custer, in mid-June 1967. Riparian habitat was composed of grasses, spearmint, yellow wood sorrel (*Oxalis stricta*), stinging nettle, and ferns; driftwood, woodpiles, and shrubs were dispersed throughout. Eleven male and three female jumping mice were trapped west of Hill City, in a marshy lowland bordering Ditch Creek. Small pools of water were interlaced with hummocks of soil that supported growths of liverworts and mosses. Grasses, sedges, and white spruce also were predominant in the immediate area. Additional specimens were obtained under similar conditions near the east end of Deerfield Lake and along Goldrun Creek, southeast of Deerfield. Representatives of *Z. h. campestris* taken near Nemo, Lawrence County, were trapped along the banks of Boxelder Creek. In these various habitats, *Sorex cinereus*, *Peromyscus maniculatus*, *Microtus longicaudus*, *M. pennsylvanicus*, and *Eutamias minimus* were trapped in association with *Z. hudsonius*.

Several jumping mice were collected in non-riparian habitats. A male from 14 mi W Hill City was trapped at the base of a large rock on a dry wooded slope that was far removed from a source of standing water. A male, from the same locality, was shot in late afternoon as it ran from beneath the branches of a partially hollow log that was situated in a dry and rocky meadow. Another male from near Nemo was trapped on a dry hillside among ponderosa pine trees and granite boulders.

About 20:30 hrs (MDT) on 1 August 1967, I heard rustling in a stand of slough grass (*Beckmannia syzigachne*) growing along the shore of the Savoy Reservoir, Lawrence County. A jumping mouse was observed climbing an already-inclined stem of grass, thus riding the stem to the ground. Straddling the bent stem and holding it close to the ground, the mouse systematically rotated the rachis and removed the seeds. Within about five minutes, the seed-laden head of the grass was bare, and the mouse departed carrying seeds in its cheeks, which were noticeably distended.

Fourteen of 31 females taken in the latter half of June carried 5.8 (4-7) embryos that were 13.1 (3-18) in crown-rump length; four others had 5.5 (4-7) placental scars. Average testicular length

of 38 males obtained in this period was 6.7 (4-10). In July, six of 23 females showed no signs of reproductive activity, but 11 pregnant females carried 6.1 (5-8) embryos which were 12.9 (3-20) in crown-rump length. The uteri of six other individuals had 3.8 (2-5) placental scars. Average length of testes of 13 males obtained in July was 6.1 (4-8). Two of six females captured early in August had 5.5 (5-6) placental scars; none was pregnant. Testicular length of six males obtained at this time was 5.7 (4-7). Most females that exhibited placental scars also were lactating.

Three young *Zapus* were captured northeast of Custer in late June. Subadults, which are brighter in color than adults and generally lack a distinctive mid-dorsal stripe, are not uncommon throughout the warm months, until at least mid-August. A female live-trapped on 25 July 1967 at the last-mentioned site gave birth to seven still-born young during the ensuing night; external measurements of these newborn young are: total length, 38.3 (37-39); tail length, 10.8 (9-13); and hind foot length, 5.0 (5).

The process of annual molt occurs in adults from mid- to late summer. For example, five males taken from 27 July to 2 August in Little Spearfish Canyon displayed bright-colored tips of new hairs projecting from beneath the old dull pelage of the dorsum. Two females from southwest of Rapid City and two males from north of Sundance (all captured in mid-August) were in completely new pelage.

Robertson (1971) recently analyzed variation in populations of *Z. hudsonius* on the Great Plains. Because his studies were concurrent with my own, and because we had a mutual exchange of information, I rely upon his results herein. Jumping mice exhibit clinal variation on the plains northwestward from eastern Kansas, becoming progressively darker in coloration and tending toward longer, narrower, deeper skulls. Robertson's findings (1971:20-21) agree with those of Krutzsch (1954:441), indicating that *Z. h. campestris*, originally described from the Black Hills, contrasts with *Z. h. pallidus* to the east in South Dakota in being conspicuously darker and averaging larger in external and cranial measurements.

Secondary sexual dimorphism is not evident in jumping mice from the study area. However, patterns of variation in size within the Hills are discernible. Individuals from Pennington County are larger than those from other Black Hills populations in occipitonasal length, zygomatic length, length of palatine foramen, and cranial depth, but are smaller in length of maxillary tooth-row, zygomatic breadth, mastoid breadth and width of palatine foramen. These dimensional relationships are reciprocal when comparing representatives from Lawrence County with those of other areas (Robertson, 1971:16-17). Physiographic irregularity of the Hills may contribute to this morphological diversity. Coloration shows no readily recognizable trends in the Black Hills.

Selected external and cranial measurements of 20 adult males, followed by those of 20 adult females, are (Robertson, 1971, Table 1): total length, 125.3±5.43, 126.2±6.86; hind foot length, 29.6±1.47, 29.5±1.64; ear length, 14.4±1.70, 13.4±1.60; occipitonasal length, 23.5±0.54, 23.2±0.46; zygomatic length, 9.5±0.25, 9.5±0.28; zygomatic breadth, 11.4±0.35, 11.3±0.39; mastoid breadth, 10.1±0.38, 10.0±0.45; interorbital constriction, 4.2±0.22, 4.3±0.20; cranial depth, 9.1±0.16, 9.2±0.27; palate length, 3.5±0.24, 3.5±0.23; length of maxillary tooth-row, 3.6±0.17, 3.5±0.15; length of palatine foramen, 4.6±0.29, 4.4±0.22; width of palatine foramen, 2.2±0.14, 2.1±0.14.

Specimens examined (207).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 9 mi S, 3 mi W Spearfish, 5000 ft, 9; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 14; 2 mi S Tinton, 6100 ft, 7; 3 mi W Nemo, 4800 ft, 1; 2 mi W Nemo, 4700 ft, 9; Nemo, 4700 ft, 1. *Pennington County:* 1 mi S, 8.5 mi W Rapid City, 2; Beaver Creek,

4 mi N, 10.5 mi W Deerfield, 6400 ft, 10; Beaver Creek, 3 mi N, 9 mi W Deerfield, 6400 ft, 1; Goldrun Creek, 1 mi S, 2 mi E Deerfield, 6400 ft, 3; Rapid Creek, 2 mi W Pactola, 4800 ft, 3 (UMMZ); Castle Rock, R. 2 E, T. 1 N, 6500 ft, 3 (UMMZ); Ditch Creek, 14 mi W Hill City, 6400 ft, 10; Ditch Creek, 13 mi W Hill City, 6400 ft, 4; Nelson's Place, 3 mi SE Hill City, 6 (UMMZ); Palmer Gulch, 4 mi SE Hill City, 6 (UMMZ); unspecified locality, 1 (UMMZ). *Custer County:* 3.5 mi S, 0.5 mi W Keystone, 5000 ft, 8; Palmer Gulch, 8 mi SE Hill City, 9 (FMNH); 5.75 mi N, 5.75 mi E Custer, 5220 ft, 42; Custer, 5 (2 AMNH, 3 USNM); Wind Cave National Park, 1 (WCNP); Game Ranch, Cold Spring Creek, Wind Cave National Park, 2 (UMMZ); Beaver Creek Canyon, Wind Cave National Park, 4200 ft, 9 (1 UMMZ).

WYOMING: *Crook County:* Bear Lodge Mountains, 6 (USNM); Bear Lodge Mountains, 6.5 mi SSE Alva, 1 (UMMZ); Bear Lodge Mountains, Warren Peak Lookout, 6000 ft, 2 (USNM); Devils Tower, flood plain Belle Fourche River, 3350 ft, 1 (USNM); 15 mi N Sundance, 2; 3 mi NW Sundance, 5900 ft, 19; Sundance, 3 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 7.

Additional records.—SOUTH DAKOTA: *Lawrence County:* Spearfish (BB). *Pennington County:* Rochford (BB). *Custer County:* Bull Springs (Bole and Moulthrop, 1942:167).

Family ERETHIZONIDAE—Porcupines

Only one genus, with one species, of this large, quilled rodent occurs in the Black Hills region.

Erethizon dorsatum bruneri Swenk

Porcupine

Erethizon epixanthum bruneri Swenk, 1916, Univ. Nebraska Studies, 16:117, 21 November (type locality, 3 mi E Mitchell, Scott's Bluff Co., Nebraska).

Erethizon dorsatum bruneri—Anderson, 1947, Bull. Nat. Mus. Canada, 102:173, 24 January.

Erethizon dorsatum occurs on the Great Plains and adjacent montane areas at sites where trees are available locally. In the Black Hills, porcupines have a wide altitudinal distribution, occurring from the boreal cap, down through the transition zone, and out onto the surrounding prairie. This rodent is active the year around. Although common in the Hills, specimens of *Erethizon* are lacking from Fall River and Weston counties.

Erethizon dorsatum bruneri differs from *E. d. epixanthum,* which occurs to the west in Wyoming, in having smaller external and cranial dimensions, arched frontals, and auditory bullae that are less inflated (Long, 1965:669).

Porcupines usually were encountered along the shoulders of highways in evening or early morning, and many specimens in collections were taken as roadkills. Due to heavy damage inflicted by this species upon potentially harvestable timber, particularly young pine trees, the U. S. Forest Service maintains a porcupine control program in the Hills. Trees with tops and branches barked indicate the abundance and widespread distribution of *Erethizon* in the study area.

Sixteen individuals were collected along Little Spearfish Canyon in late July and early August of 1967, generally along roadways at dusk. On two occasions, juvenile males were taken in company with large adult males. One procupine was shot as it persistently chewed a hole in a camper's tent; bacon grease had been spilled on the tent and even repeated attacks on the porcupine with a club could not drive the rodent away. Another individual was shot at mid-day as it roosted in the top of a pine at the bottom of Big Spearfish Canyon.

Rocky bluffs are used as den sites by *Erethizon;* dens are evident from accumulations of feces and discarded quills. Porcupine scats are in the form of pellets, which are often interconnected by strands of undigested vegetation. Frequently dens of *Erethizon* are associated with those of *Marmota flaviventris.*

A female taken near Rockerville on 29 March 1946 contained one embryo. Females obtained in July and August each showed a single placental scar in the uterine horns. A lactating female was collected northeast of Custer on 17 June 1967, and juveniles were common from July through September. The average length of testes of four males taken in August was 44.2 (40-57). Juvenile pelage

consists of fine soft blackish underfur and long yellowish guard hairs, as compared to the rather coarse underfur and whitish guard hairs of adults. The quills are less resilient than those of adults, and also possess a yellowish tinge.

Specimens examined (52).—SOUTH DAKOTA: *Lawrence County:* Big Spearfish Canyon, 3 mi W Spearfish, 4200 ft, 1; Tinton, 5900 ft, 1; 2 mi S Tinton, 6100 ft, 1; Little Spearfish Canyon, Roughlock Falls, 9 mi W Lead, 5400 ft, 1; Little Spearfish Canyon, 1 mi S, 9 mi W Lead, 5400 ft, 5; Little Spearfish Canyon, 2 mi S, 10 mi W Lead, 5800 ft, 7; Little Spearfish Canyon, 6.2 mi SW Lead, 6000 ft, 1; Little Spearfish Canyon, 12 mi S, 14 mi W Lead, 6200 ft, 2; Bogus Jim Creek, 1 (SDMT). *Meade County:* Vanocker Canyon, 3 mi S, 0.5 mi W Sturgis, 4400 ft, 1. *Pennington County:* 1.5 mi N Silver City, 1 (SDMT); 0.4 mi SW Silver City, 1 (SDMT); Rapid City, 1 (NRW); Beaver Creek, 3 mi N, 9 mi W Deerfield, 6500 ft, 1; 1 mi NW Deerfield, 1; Deerfield, 1 (SDMT); Spring Creek Canyon, 4 mi ENE Rockerville, 3600 ft, 2 (UMMZ); Ditch Creek, 14 mi W Hill City, 6400 ft, 1; 19 mi W, 3 mi S Hill City, 1; Palmer Gulch, 4 mi SE Hill City, 5300 ft, 1 (UMMZ); unspecified locality, 2 (SDSU). *Custer County:* Roby Canyon, 2 mi N, 22 mi W Custer, 5200 ft, 1; 5.75 mi N, 5.75 mi E Custer, 5220 ft, 1; Shirttail Canyon, 2 mi S Wind Cave, Wind Cave National Park, 1 (WCNP); Dewey, 11 (USNM).

WYOMING: *Crook County:* 15 mi N Sundance, 1; 15 mi ENE Sundance, 1; Sundance, Bear Lodge Mountains, 6000 ft, 1 (USNM). *Weston County:* 1.5 mi E Buckhorn, 6150 ft, 1.

Additional records.—SOUTH DAKOTA: *Custer County:* "vicinity of Otis" (Stebler, 1939:389). WYOMING: *Weston County:* "east of Newcastle" (Stebler, 1939:389).

ORDER CARNIVORA—Carnivores

A rather diverse group of mammals from the diminutive ermine to the robust grizzly bear, comprise the carnivorous fauna (nine genera and 15 species) in the Black Hills within historic time. The statuses of an additional seven species (six genera) in the Hills region remain uncertain.

Representatives of all five families of Carnivora that occur in North America either are indigenous to the Black Hills or recently have been extirpated by man. Large carnivores tend to interfere with man's pastoral enterprises, and as a result, the gray wolf, black bear, grizzly bear, mountain lion and lynx either no longer occur in the Hills, or are rare. Coyotes, badgers, and bobcats also must endure the attempts of humans to decimate their populations.

Family CANIDAE—Coyotes, Wolves, and Foxes

This family of doglike mammals is represented in the area under study by two genera and three species. Two additional canids, the swift fox and gray fox, occur in the general vicinity and may occasionally intrude into the Black Hills.

Canis latrans latrans Say

Coyote

Canis latrans Say, 1823, *in* Long, Account of an expedition from Pittsburgh to the Rocky Mountains . . ., 1:168 (footnote), (type locality, Engineer Cantonment [approximately 2 mi E Ft. Calhoun], Washington Co., Nebraska).

The coyote is known from much of North America, and is well distributed throughout the Black Hills. At least 200 individuals were poisoned on the Sheidley Cattle Company range near Rapid City in 1894 (Bailey, 1907:11), 1165 coyotes were killed in the Bear Lodge Mountains in 1907 (Bailey, 1908:6), and reports of District Rangers, Black Hills National Forest (U. S. Biological Survey files), indicate that approximately 2680 coyotes were killed in that area in the period from 1926 to 1935. From 1962 to 1968, bounties on 1930 coyotes were paid by the counties that comprise the South Dakotan portion of the Hills (records from South Dakota Dept. Game, Fish and Parks), and extensive use of 1080 poison (sodium monofluoracetate) has further reduced the population in the eastern and southern sections of the Black Hills (A. H. Richardson, pers. com.). In spite of these attempted control measures, *Canis latrans* seems to be increasing in abundance in the northern Hills, especially along the South Dakota-Wyoming border (A. W. Jones, pers. com.).

Compared to *Canis latrans lestes*, which occurs to the west in Wyoming, *C. l. latrans* is slightly smaller externally and cranially, and the upper parts are much paler in color (Long, 1965:674).

Evidently, coyotes increasingly invaded the Black Hills as gray wolves were extirpated by man, and became much more abundant as the latter species was reduced in numbers. Grinnell (1873: 79-80) stated: "The coyote was found in considerable numbers on the plains, and was especially abundant among the elevated table-lands that were crossed just before reaching the Black Hills. After penetrating into the hills proper, however, I did not see a single specimen until I left them for the Big Cheyenne [Cheyenne River], when I again noticed coyotes in numbers. In the Black Hills, this species would seem to be replaced by the preceding [gray wolf]." In 1894, W. W. Granger indirectly referred to a change in relative abundance of the two species when he noted that gray wolves were "not uncommon," and coyotes were "common" in the Black Hills (J. A. Allen, 1895a:274). Coyotes continued to increase in numbers in the Hills after the turn of the century, whereas the gray wolf was eliminated shortly thereafter. Conversely, the decline in ungulate populations, important as a source of food for coyotes, and increased conflict with the agricultural pursuits of man, caused a reduction in the number of *C. latrans* on the plains.

I often have observed *C. latrans* near dusk and shortly after dawn in the various prairie dog towns in Wind Cave National Park. On 25 July 1968, I watched a large adult "mousing" along Highland Creek for several hours in midmorning. A litter was raised in Beaver Creek Canyon that summer and the pups were vocally active each evening. On 27 August 1968, an adult coyote and three young were observed pursuing a doe pronghorn in Shirttail Canyon. The fate of the pronghorn remains unknown as all animals quickly passed from view; however, no evidence of its capture could be found in the subsequent inspection along the route of the chase.

Reproductive data applicable to the Black Hills coyote population were obtained from the U. S. Biological Survey files. Two females taken near Custer in March 1944 carried four and seven embryos, respectively; nine females obtained in the Hills in late April and early May had an average of 6.4 (4-7) embryos each. Two adult females (one with seven suckling pups and the other with four embryos) were captured in Wind Cave National Park late in April 1918 by Troy C. Beach. Thus, coyotes in the Black Hills, as elsewhere on the northern plains, apparently breed in February and March, bearing litters in April and May (Mengel, 1971:325).

Stomachs of five coyotes, trapped in Wind Cave National Park in early June 1924, contained the remains of domestic chicken, domestic lamb, and cottontail rabbit (*Sylvilagus* sp.).

Specimens examined (19).—SOUTH DAKOTA: *Pennington County:* 4 mi S, 14 mi W Hill City, 2. *Custer County:* 18 mi NE Dewey, 4 (USNM); 12 mi NE Dewey, 1 (USNM); 4 mi N Dewey, 1 (USNM); 5 mi NW Wind Cave, 1 (WCNP); Wind Cave Canyon, Wind Cave National Park, 1 (WCNP); Shirttail Canyon, Wind Cave National Park, 2 (WCNP); 3 mi SE Wind Cave, 1 (WCNP). *Fall River County:* 5 mi W Minnekahta, 1.

WYOMING: *Crook County:* Bear Lodge Mountains, 2 (USNM); Grand Canyon, Sundance, 1 (USNM); Rattlesnake Canyon, Sundance, 1 (USNM).

UNSPECIFIED LOCALITY: Black Hills, 1 (SDSU).

Additional records (USBS card files unless otherwise noted).—SOUTH DAKOTA: *Lawrence County:* Spearfish; Lead. *Meade County:* Piedmont. *Pennington County:* Rochford; Deerfield; 17 mi NW Custer. *Custer County:* Bull Springs, 14 mi NW Custer (Lamster, 1943: 1); Custer; 9 mi W Pringle; Pringle; Dewey; 18 mi W Custer; unspecified locality, 1 (Jackson, 1951:262). *Fall River County:* Hot Springs; Minnekahta.

Canis lupus irremotus Goldman

Gray Wolf

Canis lupus irremotus Goldman, 1937, Jour. Mamm., 18:41, 14 February (type locality, Red Lodge, Carbon Co., Montana).

The gray wolf formerly occurred throughout much of the United States. Historical reports indicate that *Canis lupus* previously was abundant and widely distributed on the Great Plains and in the Black Hills. Extirpation of the vast herds of bison destroyed the main food source of the wolf and this, along with trapping and poisoning of wolves for protection of livestock, for fur, and for bounties, finally led to the elimination of this species from major areas of its former range.

Canis lupus irremotus differs from *C. l. nubilus* to the south and east in being larger, paler, and narrower in the frontal region, especially relative to the width of the rostrum (Long, 1965:677). Goldman (1944:448-449) noted that specimens from the Black Hills are variable and grade toward *nubilus*.

Grinnell (1875:79) wrote of this species as follows: "I found the gray wolf one of the most common animals in the Black Hills, and hardly a day passed without my seeing several individuals of this species. They were generally observed singly or by twos and threes, sneaking along the mountain sides or crossing the narrow valleys." He indicated that in the Black Hills, *C. latrans* (see account of this species) was replaced by *C. lupus*. Dodge (1876:133) noted: "The wolves are of enormous size, a very dark gray in color, and in considerable numbers." From the spring of 1895 to the autumn of 1897, about 500 gray wolves were killed on the range of the Ames Cattle Company (5435 square miles) in northeastern Crook County, Wyoming (Long, 1965:676). J. T. Craig, manager of Western Ranches Limited, Belle Fourche, South Dakota, filed a report with the U. S. Biological Survey in 1896, indicating that *C. lupus* was responsible for a three percent loss of calves, one percent loss of adult cattle, and five percent loss of colts annually (Young, 1946a:122). G. E. Lemmon, manager of the Sheidley Cattle Company, Rapid City, South Dakota noted that 80 to 100 gray wolves were poisoned on the range of this company in 1896 (Bailey, 1907:11). Near Newcastle, wolves were still numerous enough to be destructive to livestock in 1905 and 1906 (Bailey, 1907:10). Evidently, the gray wolf was already becoming more scarce at this time, whereas the coyote was becoming more abundant in the Black Hills (see Allen, 1895a:274).

Decimation of *C. lupus* in the Hills continued during the early part of the twentieth century (U. S. Biological Survey files, unless otherwise noted). About 925 gray wolves were obtained by the U. S. Forest Service in the Bear Lodge Mountains and surrounding portions of Crook County, Wyoming, in 1907 (Bailey, 1908:6). Bounties were paid in 1911 on 55 wolves by counties that comprise the South Dakotan section of the Hills (records from South Dakota Dept. Game, Fish, and Parks). Eight wolves were destroyed in 1915, and five more were killed in 1916. A pregnant female that carried four embryos was taken 18 mi NE Dewey on 25 March 1917. A male was killed 15 mi SE Dewey on 10 November 1920. Three individuals were shot on 23 December 1926, and two were taken on 11 January 1928.

One of the famous American renegades was the "Custer Wolf" which ranged in the vicinity of Custer for a period of seven years (Young, 1946a:68, photo opposite). This large male had a known range of 40 by 60 miles (Seton, 1929a:257) and was credited with killing $25,000 worth of livestock during this period. It avoided capture despite a bounty of $500 offered for its scalp. A Federal Hunter, H. P. Williams, concentrated entirely upon the "Custer Wolf" from March to October 1920 before finally succeeding in killing it (Young, 1944:277). The last specimen from the Black Hills known to me is one reported by the District Forester in Harney National Forest, 30 January 1934 (U. S. Biological Survey files). On 4 July 1967, I found a mandible of *C. lupus* in a woodrat nest at the rear of Davenport Cave, southwest of Sturgis. Currently,

the former range of *C. lupus* in the Black Hills has been pre-empted by *Canis latrans*.

Specimens examined (3).—SOUTH DAKOTA: *Meade County:* Davenport Cave, 3 mi S, 1.5 mi W Sturgis, 4400 ft, 1. *Custer County:* 12 mi NE Dewey, 1 (USNM).

WYOMING: *Crook County:* Sand Creek Canyon, 1 (USNM).

Additional records.—SOUTH DAKOTA: *Custer County:* 18 mi NE Dewey (USBS files); Dewey (Goldman, 1944:445). *Fall River County:* 15 mi SE Dewey (USBS card files). WYOMING: *Crook County:* northeastern portion of county (Long, 1965:676).

Vulpes vulpes regalis Merriam

Red Fox

Vulpes regalis Merriam, 1900, Proc. Washington Acad. Sci., 2:672, 28 December (type locality, Elk River, Sherburne Co., Minnesota).

Vulpes fulva regalis—B. Bailey, 1929, Jour. Mamm., 10:157, 9 May.

The red fox is widely distributed and relatively common in the eastern Great Plains, and occurs sparingly in suitable habitat in the eastern and southern portions of the Black Hills. Grinnell (1875: 96) observed three red foxes, an old female and two young that inhabited a burrow on the edge of a prairie dog town along the northern fringe of the Black Hills in 1874. Bailey (1888:432) witnessed "a few tracks" of this species in the snow in October 1887, and on 20 July of the following year obtained a female near Custer, noting a field report to the U. S. Biological Survey that this species was "common" in that vicinity. A male was taken by Merritt Cary near Elk Mountain on 16 October 1903.

Game Biologists A. H. Richardson and L. Petersen, and Game Warden E. L. Woods, indicated to me that *Vulpes vulpes* was relatively unknown in the Black Hills five to 10 years ago, but that since 1965 it has increased noticeably in the region (pers. com.). These naturalists felt that the coyote population has decreased considerably in some areas of the Black Hills because of extensive use of 1080 poison, and that the red fox is replacing the coyote in the southern and eastern sections (see additional records for specimens that recently have come to the attention of these men).

A red fox recently was taken along the southern periphery of the Black Hills at a locality 10 mi N Rumford, Fall River County (Jones and Henderson, 1963: 283). From 1962 to 1968, bounties on 1079 *V. vulpes* have been paid by those counties that comprise the South Dakotan portion of the Black Hills (records from South Dakota Dept. Game, Fish, and Parks).

Vulpes vulpes regalis differs from *V. v. macroura* of western Wyoming in being larger and more golden-reddish instead of yellowish in color (Long, 1965:679). As other recent authors, I follow Churcher (1959) in using the specific name *Vulpes vulpes* (Linnaeus) for American red foxes.

Specimens examined (2).—SOUTH DAKOTA: *Custer County:* Custer, 1 (USNM); Elk Mountain, 1 (USNM).

Additional records (A. H. Richardson, L. Petersen, and E. L. Woods, pers. com.).—SOUTH DAKOTA: *Lawrence County:* near Nemo, 1. *Pennington County:* 7 mi NW Rapid City, 1. *Custer County:* 2 mi S Custer, 1; 2 mi W Hermosa, 1. *Fall River County:* 2 mi N Hot Springs, 1; 2 mi S Hot Springs, 1.

Family URSIDAE—Bears

The large omnivorous ursids are represented in the Black Hills by one genus and two species.

Ursus americanus americanus Pallas

Black Bear

Ursus americanus Pallas, 1780, . . . Spicilegia zoologica . . ., fasc. 14.5 (type locality, eastern North America).

Although I have examined but a single specimen of this species, historical accounts as well as recent newspaper accounts and reports by National Forest Service personnel, indicate the presence of this bear in the Black Hills.

Dodge (1876:132) wrote of bears in the Black Hills as follows: "The country in this part of the Hills [along Rapid and Boxelder Creeks in Pennington County] is full of bear sign. In some places almost

a quarter of an acre will be rooted up as if by hogs; small thickets of berry-bearing bushes are torn and broken; ant-hills are dug into and huge logs turned over by this omnivorous monster in search of his food." He (1876:133) continued, . . . seven or eight bears were killed by our whole party . . . from the little black to the mammoth grizzly." Indians told Hoffman (1877:97) that the only place the black bear was encountered was in the Black Hills and in the Bighorn country. Bailey (1888:432) mentioned that three kinds of bears (black, brown, and silvertip) "were said to occur" in the Hills.

On 2 September 1968, a 160 pound domestic ewe, with its throat slashed and flesh eaten from its back, shoulders, and hindquarters, was found in Swede Gulch, on the Philip Wolfe ranch, 2 mi N and 5 mi W Rochford, Pennington County (Rapid City Journal, 3 September 1968, p. 2). On the stream bank beside the ewe was the distinctive print of a bear. In November of the same year a 300-pound adult male black bear was shot west of Rochford, between Black Fox Campground and Crook's Tower.

Mr. Raymond Nilles, Forest Ranger of the Sundance District, told me of finding huge, deep claw marks on a tree along Hershey Creek in the northern Hills in 1966. The claw marks began about six feet from the base of the tree and extended to the ground; Mr. Nilles and others credit these markings to the activity of a bear. Other recent reliable sightings of black bear in the Black Hills are as follow: Big Spearfish Canyon; along Cold Creek, in Lawrence County; near Redfern; in Beaver Creek Valley, in Pennington County; and at Camp Mallo in Weston County. It should be noted that captive black bears are tourist attractions in the Black Hills region, and some of these may occasionally escape.

Specimen examined (1).—SOUTH DAKOTA: *Pennington County:* west of Rochford, 1 (mounted and on display at Wall Drug Store, Wall, South Dakota).

Ursus arctos horribilis Ord

Grizzly Bear

Ursus horribilis Ord, 1815, *in* Guthrie, a new geographical, historical, and commercial grammar . . ., ed. 2, 2:291, 299 (type locality, north side of Missouri River, near mouth of Wolf Creek, Roosevelt Co., Montana).

Ursus arctos horribilis—Erdbrink, 1953, A review of fossil and recent bears of the Old World. . . . Jan de Lange, p. 339, 30 March.

Ursus rogersi bisonophagus Merriam, 1918, N. Amer. Fauna, 41:66, 9 February (type locality, Bear Lodge Mountains, Sundance National Forest, Black Hills, Crook Co., Wyoming).

In discussing the Black Hills in 1851, a trapper indicated that "Grizzly bears are found there sometimes in bands like buffalo. . . ." (Culbertson, 1952:90). Although not quite as enthusiastic, Grinnell (1875:81), Dodge (1876:132-133), and Bailey (1888:432) each alluded to the presence of large numbers of grizzly bears in the Black Hills in the late 1800's. The four specimens examined all were taken in the study area between 1855 and 1887. On 7 August 1874, General Custer and Colonel Ludlow shot a well-scarred old male near Nahant (about three miles south of the present town of Dumont, Lawrence County, South Dakota); soon after, other members of the expedition killed a cinnamon-colored grizzly in the same area (Winchell, 1875: 50; O'Hara, 1929:251-252). The male was a deep, glossy black, except for a sprinkling of dark gray hairs on the head, lower parts of the shoulders, and thighs (Grinnell, *loc. cit.*). Two Indian scouts killed an old female and two cubs a few days later much farther eastward (along Boxelder Creek, Lawrence Co., South Dakota). "The cubs were about half grown, and with the mother, were of a yellowish clay color. The inner half of each hair was deep black, but the outer extremity was a bright reddish-yellow. This gave them a curious mottled appearance and induced many of those who saw them to consider them a different species from the one killed by General Custer" (Grinnell, *loc. cit.*).

The foregoing account points out the extreme amount of individual variation found among this species, and the taxonomic dilemma thus implied. At the moment, there are about 96 named kinds of grizzly bears, most of which can be attributed to the work of C. Hart Merriam. Merriam (1918:66) described *Ursus rogersi bisonophagus* from the Bear Lodge Mountains, and at the same time (1918:93) included the Black Hills within the range of *Ursus absarokos.* I follow Erdbrink (1953:339), who regarded the brown bear of the Palearctic and Nearctic regions as being conspecific and therefore employed the name *Ursus arctos horribilis.* Professor E. Raymond Hall, of The University of Kansas, currently is reviewing the taxonomic status of the grizzly bear. The following selected cranial measurements of grizzlys from the Hills were taken by Professor Hall, and are the average (extremes) of three females and a male (type of *U. r. bisonophagus*), all fairly young animals: occipitonasal length, 281.3 (255.0-322.0); palatal length, 166.5 (157.0-180.0); interorbital breadth, 70.5 (63.2-79.4); length of P4-M2, 72.2 (68.0-76.2); length of M2, 36.5 (33.7-38.4); breadth of M2, 18.1 (17.2-19.7).

Green (1961:147, 1962:3) recently located a partially fossilized arthritic skeleton of a grizzly in a cave near Hot Springs, Fall River Co., South Dakota. It should be noted that all reports of bears in the Black Hills region since the turn of the century have been credited to *U. americanus* rather than *U. arctos;* evidently, even though rare in occurence, the former has replaced the latter in recent historic time.

Specimens examined (4).—WYOMING: *Crook County:* Bear Lodge Mountains, 1 (USNM); Sundance National Forest, 3 (USNM).

Family PROCYONIDAE—Raccoons

Only one procyonid species, the raccoon, is distributed in the Black Hills. The raccoon is an economically important mammal. Its pelt is marketable and its flesh eaten by humans; it provides much recreation as a hunted fur-bearer, and accounts for substantial loss of certain crops to farmers annually. The species probably is commoner in the region now than in the recent past.

Procyon lotor hirtus
Nelson and Goldman

Raccoon

Procyon lotor hirtus Nelson and Goldsmith, 1930, Jour. Mamm., 11:455, 11 November (type locality, Elk River, Sherburne Co., Minnesota).

Procyon lotor is common and widespread in suitable habitat throughout North America. Although few actual specimens have been taken, the species is common in the Black Hills. Usually the raccoon is found along streams, around lakes and marshes, and is a frequent nocturnal visitor to area campgrounds.

Procyon lotor evidently is a recent addition to the Black Hills mammalian fauna. Hayden (1859:706, 1862:143) noted that this species was seldom seen beyond the frontier in the mid-nineteenth century, and indicated that, although a few had been observed in the White River Valley, the raccoon seldom passed up the Missouri River above latitude 42°. Grinnell (1875) and Dodge (1876) did not include the raccoon in their respective lists of mammals encountered by early expeditions to the Black Hills region.

A careful search of the mud banks of almost any riparian community in the Hills will reveal the presence of tracks of *P. lotor.* While camping in Little Spearfish Canyon in early August 1967, my cooking supplies were raided each night by a large male of this species. A huge steel trap, anchored by a heavy chain and baited with carcass of a chipmunk, finally captured the raccoon, but it escaped, dragging the trap behind. One week later a local fisherman found the animal, with the trap and chain still attached, drowned in Little Spearfish Creek. An adult *Procyon* and four ju-

veniles were observed in the area of Roughlock Falls on 7 August of the same year. Another individual was a nightly visitor at the Boxelder Creek Campground, just west of Nemo, in late June 1967. Specimens of this species obtained in the vicinity of Hill City were taken along a small tributary in a spruce canyon.

Specimens examined (4).—SOUTH DAKOTA: *Lawrence County:* 2 mi S, 10 mi W Lead, 5800 ft, 1. *Pennington County:* 4 mi SE Hill City, 5300 ft, 1 (UMMZ); S Hill City, 1 (UMMZ). *Custer County:* Wind Cave National Park 1 (WCNP).

Additional records.—SOUTH DAKOTA: *Custer County:* Custer State Park (USBS card files). WYOMING: *Crook County:* New Haven (Goldman, 1950:38).

Family MUSTELIDAE—Weasels, Skunks, and Allies

Three genera and six species of weasel-like mammals inhabit the Black Hills; the occurrence of four additional genera (five species) in the general area remains uncertain. Members of this family mainly are terrestrial, but two (the badger and black-footed ferret) are semifossorial in habit, and one (the mink) is equally at home on land or in water. Breeding female mustelids generally exhibit induced ovulation, delayed implantation, and are monestrous. Both sexes possess anal scent glands, of which those of weasels, mink and skunks are the most noisome to humans.

Mustela erminea muricus (Bangs)

Ermine

Putorius (*Arctogale*) *muricus* Bangs, 1899, Proc. New England Zool. Club, 1:71, 31 July (type locality, Echo, 7500 ft, El Dorado Co., California).

Mustela erminea murica—Hall, 1945, Univ. of Kansas Publ., Mus. Nat. Hist., 25:84, 27 February.

Mustela erminea muricus is distributed throughout the northwestern quarter of the United States; in the Black Hills it is most common in lower spruce-aspen parklands, streamside coniferous forest, and grassy to semi-swampy woodlands, usually at altitudes above 5000 feet. This small weasel is rather uncommon in collections due to its seclusive habits and is known only from Pennington and Custer counties in the South Dakotan portion of the Hills, but from both counties of the Wyoming section. Hall (1951:164-165) first reported this species from the study area.

Ecological data concerning the ermine in the Black Hills are rather meager. During the winter months of 1945-1946, J. A. King captured five individuals (two males and three females) in the central Hills in box traps. The traps were placed in aspen groves and along marshes bordering small tributaries that flowed through canyons dominated by spruce. One female that was kept as a pet by King, carried four embryos when she died on 30 March 1946. Two females were obtained in mid-July of 1965 on a huge dirt slide, overgrown with grass and small aspen, situated between two high, rocky outcrops east of Four Corners, Wyoming. One had raised a litter shortly before capture; three old placental scars were present and mammary tissue was receding. The other was a subadult, possibly a young of the first female. Coats (1945:10) captured 16 ermine one winter in the vicinity of Hill City.

Individuals taken in the warmer months (June and July) were in brown summer pelage and those obtained in colder months (November to January) were in white winter pelage. Three ermines that died in March were molting from winter to summer pelage; two of these had been kept as pets by King since mid-January, and were in the 21st day (UMMZ 90189) and 37th day (UMMZ 90190) of molt, respectively, at time of death.

Specimens examined (12).—SOUTH DAKOTA: *Pennington County:* Palmer Gulch, 3 mi SE Hill City, 5300 ft, 2 (UMMZ); Pflander's Ranch, 3 mi SSE Hill City, 5300 ft, 1 (UMMZ); Nelson's Place, 4 mi SE Hill City, 5300 ft, 1 (UMMZ); Spring Creek, south of Rapid City, 2 (MHM); Spring Creek, 2 mi W Oreville, 5500 ft, 1 (UMMZ). *Custer County:* 0.5 mi E Sylvan Lake, 6250 ft, 1 (UMMZ).

WYOMING: *Crook County:* 3 mi NW

Sundance, 5900 ft, 1. *Weston County:* 4 mi E Four Corners, 6000 ft, 2.

UNSPECIFIED LOCALITY: Black Hills, 1 (SDSU).

Mustela frenata alleni (Merriam)

LONG-TAILED WEASEL

Putorius alleni Merriam, 1896, N. Amer. Fauna, 11:24, 30 June (type locality, Black Hills, Custer, Custer Co., South Dakota).

Mustela frenata alleni—Hall, 1936, Carnegie Inst. Washington Publ., 473:106, 20 November.

The long-tailed weasel occurs throughout the United States. In the Black Hills it inhabits brushy areas, woodlands, and rock piles, usually above 5000 feet and near a source of permanent water. The species evidently is rather uncommon in the Hills, being presently known only from Pennington, Custer, and Crook counties. This mustelid was first recorded from the study area by Vernon Bailey (1888:433).

As presently understood, *Mustela frenata alleni* is confined to the Black Hills of South Dakota and Wyoming. Hall (1951:276) recorded *alleni* from Mitchell, Scott's Bluff Co., Nebraska, but Jones (1964:270) subsequently assigned these specimens to the subspecies *longicauda.* Specimens from northwestern Nebraska, and one from Rapid City, Pennington Co., South Dakota, undoubtedly represent intergrades between *alleni* and *longicauda.*

Mustela frenata alleni differs from *M. f. longicauda,* which occurs to the north, east and south of the Black Hills, in possessing smaller cranial and external dimensions. *Mustela frenata nevadensis,* known from the west in Wyoming, averages slightly larger in size and is a darker brown in summer pelage than is *M. f. alleni* (Long, 1965:693).

Ecological data are essentially lacking for this species in the Black Hills. In November 1887, Vernon Bailey caught a long-tailed weasel in a trap baited with a prairie dog and set on a creek bank near Rapid City. During the summer of 1968, individuals were observed along stream drainages, brushy ravines, and around headquarters buildings in Wind Cave National Park, but no specimens were obtained. J. A. King captured a male in an aspen thicket southeast of Hill City in January of 1946; this individual was retained in captivity until 9 April. King noted that molt from white winter pelage to brown summer pelage commenced about 4 February; thus, when the male (UMMZ 90209) died, it was in the 64th day of pelage replacement and long white guard hairs were still present over shoulders and neck. Bailey (*loc. cit.*) noted that the November-taken individual ". . . is just changing from the brown coat to the white, and is a little more than half white. The brown hairs come out very easily; the white hairs are firm." He also witnessed a few tracks along creeks and ventured that long-tailed weasels were quite common in the general area.

Specimens examined (13).—SOUTH DAKOTA: *Pennington County:* Hill City, 1 (AMNH); Palmer Gulch, 3 mi SE Hill City, 1 (UMMZ); 20 mi N Elk Mountain, 6000 ft, 1 (USNM). *Custer County:* Palmer Gulch, 8 mi SE Hill City, 5300 ft, 4 (FMNH); Bull Springs, 2 mi N, 9 mi W Custer, 1 (UMMZ); Custer, 3 (2 AMNH, 1 USNM).

WYOMING: *Crook County:* Bear Lodge Mountains, 3 mi N Sundance, 5500 ft, 1 (USNM); Sundance, 1 (USNM).

Mustela nigripes (Audubon and Bachman)

BLACK-FOOTED FERRET

Putorius nigripes Audubon and Bachman, 1851, The viviparous quadrupeds of North America, 2:297 (type locality, Ft. Laramie, Goshen Co., Wyoming, according to Hayden, Trans. Amer. Philos. Soc., 12 (n. s.): 138, 1863).

Mustela nigripes—Miller, 1912, Bull. U. S. Nat. Mus., 79:102, 31 December.

Presently on the list of endangered species, the black-footed ferret is among the rarest of North American carnivores. This mustelid is characteristic of short and mid-grass prairies, and its geographic range is generally coincident with that of the sciurid genus *Cynomys.* Although ferrets utilize alternate sources of food (Cahalane, 1954:423; Hillman, 1968:6; Henderson *et al.,* 1969:22-24), prairie

dogs are its primary prey and burrow systems of the latter species are inhabited by ferrets.

Mustela nigripes currently seems to be holding its own in western South Dakota, but changing land use and man's effort to control prairie dog populations through destruction of thousands of dog towns have adversely affected the distribution and abundance of black-footed ferrets throughout its range. For example, widespread use of compound 1080 to eradicate *Cynomys* is a potential threat to the survival of ferrets. Hillman (1968:11-12) has shown that consumption of 1080-poisoned prairie dogs by black-footed ferrets can cause fatal secondary poisoning.

Henderson *et al.* (1969:31-37) recently summarized the distributional status of *M. nigripes* in South Dakota. His census was based on questionnaires given to land owners, on a survey of published literature and unpublished records such as those located in the U. S. Biological Survey files, and on examination of specimens housed in various museums. Although the species was not uncommon on the prairie along the eastern periphery of the Hills, only a few records are directly applicable to the Black Hills proper.

In 1903-1904, James P. Campbell observed a ferret in a prairie dog town in Gillette Canyon, northeast of Elk Mountain, Custer County. Another individual was observed running along a road located in T. 2 S, R. 5 E, 5800-6000 feet, Custer County, by James Clark in July 1965; this site may be within the foothill region of Custer State Park, where habitat would be suitable for ferrets.

Troy C. Beach observed a *M. nigripes* in a prairie dog town in Wind Cave National Park in the spring of 1922. Upon completion of filming "The Vanishing Prairie," Walt Disney Productions, Inc., released two males and one female in the National Park on 30 December 1953 (Cahalane, 1954:424; Garst, 1954: 594). These were three of five ferrets (an adult and four young) trapped in a dog town 2 mi W Midland, Haakon Co., South Dakota, by Mr. George Barnes early in August 1953 (Garst, *loc. cit.*). Subsequently, a Park Naturalist noted a ferret in the vicinity of Norbeck Dam on 27 August 1956. The last actual sightings of this species in the Park were in 1957 (Wind Cave National Park files). When excavating prairie dog burrows, ferrets form a characteristic trench-like structure from three to five inches in width and from one to nine feet in length (Henderson *et al.*, 1969:16). In 1969, the diagnostic trench of a black-footed ferret was noted in a dog town in Wind Cave National Park. Restocking of *M. nigripes* in the National Park, and in other sanctuaries where prairie dogs thrive, such as Custer State Park and Devils Tower National Monument, could insure the survival of this interesting mammal.

Little is known concerning the reproduction of the black-footed ferret but young evidently are born in spring and first emerge above ground early in July, at which time family groups are most frequently observed in western South Dakota.

Specimens examined (4).—SOUTH DAKOTA: *Pennington County:* Spring Creek, south of Rapid City, 2 (MHM).

WYOMING: *Weston County:* Newcastle, 2 (USNM).

Additional records.—(see text and Henderson *et al.*:31-37, Appendix II).

Mustela vison letifera Hollister

MINK

Mustela vison letifera Hollister, 1913, Proc. U. S. Nat. Mus., 44:475, 18 April (type locality, Elk River, Sherburne Co., Minnesota).

Mink live along streams, edges of ponds, marshes, and lakes in all but the southwestern part of the United States. Uncommon in collections due to its valuable pelt, *Mustela vison* is fairly abundant along water courses throughout the Black Hills. For example, "numerous mink" are trapped near Sturgis annually (South Dakota Conservation Digest, 23: 12, March 1956).

Grinnell (1875:80) saw no living specimens while in the Hills, but observed signs of mink along streams and saw a skin that the owner said had been taken "in the Black Hills." Bailey (1888: 433) noted the presence of this species in the Hills in November 1887.

A lactating female was taken along the edge of a beaver pond south of Tinton on 16 July 1961 by W. C. Stanley; to my knowledge, no additional data are available for this species from the Black Hills, save for the specimens listed below.

Specimens examined (4).—SOUTH DAKOTA: *Lawrence County:* 2 mi S Tinton, 6100 ft, 1. *Pennington County:* Rapid City, 1; Martindale Ranch, 0.5 mi E Rapid City, 1 (SDMT); Spring Creek, south of Rapid City, 1 (MHM).

Taxidea taxus taxus (Schreber)

BADGER

Ursus taxus Schreber, 1778, Die Saugthiere . . ., description on pp. 520-521 (type locality, Labrador and Hudson Bay, restricted southwest of Hudson Bay by Miller and Kellogg, Bull. U. S. Nat. Mus., 205:747, 3 March 1955).

Taxidea taxus—Rhoads, 1894, Amer. Nat. 28: 524, June.

Taxidea taxus is a relatively common inhabitant of the Northern Great Plains surrounding the Black Hills, where it occurs throughout the Red Valley "racetrack," Wind Cave National Park, and other areas where fringes of prairie impinge upon the foothills. Being a rapid and powerful digger, the badger provides reliable evidence of its presence by its characteristic excavations and den sites, usually located on gently sloping hillsides.

The genus *Taxidea,* with but one Recent species, is distributed in central and western North America. Some years ago, Viola S. Schantz began a revision, naming 10 new subspecies over a period of several years, but a final report was not issued; Charles A. Long currently is analyzing geographical variation of *Taxidea taxus.* Schantz (1946:81) described *T. t. dacotensis* from Folsom, Custer Co., South Dakota, just east of the Black Hills, and included specimens from the Hills under that name. Because of the great individual variation in the species and because an adequate number of specimens for analysis is lacking, I tentatively follow Hall (1936) in assigning the Black Hills specimens to *Taxidea taxus taxus.*

The badger is rather uncommon in the Black Hills proper. Cahalane (1948: 249; 1951:209) reported that a pair was released about 1940 in Wind Cave National Park, where thriving prairie dog towns offer an ample food supply, and that this pair produced at least one litter of young. Koford (1958:31) noted that several prairie dog tunnel systems in Shirttail Canyon had been excavated by badgers in 1955. In the early morning of 9 July 1968, I observed an adult female and two pups digging out a *Cynomys* burrow on Bison Flats, in the National Park; a Ranger-Naturalist at the Park observed a female badger carrying a young pup in her mouth near that prairie dog town on 20 May 1957 (Wind Cave National Park files). An adult *T. taxus* was observed along the road 6 mi NW Spearfish on 5 August 1969 eating a road-killed *Sciurus niger.*

Bounty claims were paid in 1962 on 37 badgers taken in the counties that comprise the South Dakotan portion of the Black Hills (records from South Dakota Dept. Game, Fish and Parks). One individual trapped in the winter of 1964-65 southwest of Hill City was taken at an elevation in excess of 6000 feet.

Specimens examined (6).—SOUTH DAKOTA: *Meade County:* 5.6 mi N Piedmont, 1 (SDMT). *Pennington County:* near Rapid City, 1 (FMNH); Spring Creek, south of Rapid City, 1 (MHM); 4 mi S, 14 mi W Hill City, 1. *Custer County:* Dewey, 2 (USNM).

Mephitis mephitis hudsonica Richardson

STRIPED SKUNK

Mephitis americana var. *hudsonica* Richardson, 1829, Fauna Boreali-Americana, 1:55 (type locality, plains of Saskatchewan, Canada).

Mephitis mephitis hudsonica—Hall, 1934, Univ. California Publ. Zool., 40:368, 5 November.

The striped skunk occurs throughout the United States. In the Black Hills, it

ranges from the lower elevations of the surrounding plains, through the foothill transition zone, up to altitudes of about 6200 feet. The species is at home in a variety of habitats, but prefers forest borders, wooded ravines, rocky outcrops, and brushy agricultural fields with associated fencerows. It is no stranger to the habitations of man, and although represented in museum collections by only a few specimens, the species is common throughout the Black Hills region. Grinnell (1875:80) first noted the presence of this mustelid in the Hills.

Striped skunks often were observed along roadsides and in the vicinity of campgrounds. Residents of Nemo, Lawence County, indicated that more than 70 individuals had been killed in the community dump in 1966-1967; an adult female and an immature female were obtained there on 30 June 1967. Bailey (1888:433) captured an individual near Rapid City in a trap baited with the carcass of a prairie dog. Most remaining specimens taken in the Black Hills have been either killed on roads, or represent skeletal material found in caves and rocky crevices.

A juvenile was captured on 8 August 1894 at Custer by W. W. Granger. Another immature *Mephitis* that was obviously sick was captured along a road northwest of Minnekahta on 16 June 1967. This individual offered no resistance; possibly it had been poisoned or was rabid. A female taken near Nemo on 30 June had five placental scars, two in the right uterine horn, and three in the left.

Specimens examined (30).—SOUTH DAKOTA: *Lawrence County:* Nemo, 4700 ft, 2. *Pennington County:* near Rapid City, 8 (FMNH); Moon, 22 mi W Hill City, 6200 ft, 1; Ditch Creek Valley, 14 mi W Hill City, 6400 ft, 1; Hill City, 4975 ft, 2; Spring Creek, 3 mi E Hill City, 1 (UMMZ); Spring Creek, south of Rapid City, 1 (MHM); 20 mi N Elk Mountain, 1 (USNM). *Custer County:* Custer, 3 (1 USNM, 2 AMNH); south of Otis, 1 (UMMZ); Wind Cave National Park, 1 (WCNP); Elk Mountain, 1 (USNM); Dewey, 3 (USNM). *Fall River County:* 1.75 mi N, 4.5 mi W Minnekahta, 3800 ft, 1; 5.5 mi E Minnekahta, 4000 ft, 2.

WYOMING: *Crook County:* 3.5 mi NW Sundance, 5000 ft, 1.

Additional record—SOUTH DAKOTA: *Fall River County:* Minnekahta (USBS card files).

Family FELIDAE—Cats

Of the three felids that occur in the Black Hills, bobcats are by far the most common; mountain lions are less frequent, and lynx are but rare visitors to the region in recent years.

Felis concolor hippolestes Merriam

Mountain Lion

Felis hippolestes Merriam, 1897, Proc. Biol. Soc. Washington, 11:219, 5 July (type locality, Wind River Mountains, near head Big Wind River, Fremont Co., Wyoming).

Felis concolor hippolestes—Nelson and Goldman, 1929, Jour. Mamm., 10:347, 11 November.

Previously, *Felis concolor* occurred through much of North America, but it has been extirpated in many parts of its range and now occurs primarily in regions poorly populated by humans. The mountain lion feeds principally on deer and occasionally upon livestock. Due to its role as a large predator, this species has been persecuted to the point that even within its present range, it is now rare and should be protected. *Felis concolor* is native to the Black Hills, although it is uncommon and inhabits the more remote and rugged areas.

Members of the Custer Expedition of 1874 saw but one "panther," near the head of Castle Creek (O'Hara, 1929: 252). Grinnell (1875:79), who accompanied Custer, believed that these felids were quite numerous and saw indications of their presence on several occasions: "I . . . once found the partially devoured remains of a deer thad had just been left by one of these animals." Members of the Newton-Jenney Survey observed two or three mountain lions but none was killed (Dodge 1876:133). A female mountain lion and two young were shot in November 1887, just after the adult had killed a large mule deer buck (Bailey, 1888:431) and Merritt

Cary obtained a female near the head of Bear Creek in the Bear Lodge Mountains in 1890.

Earl Bedell shot a lion near the head of Stockade Beaver Creek, Weston Co., Wyoming, in 1930 (Mann, 1959:3) and a female *F. concolor* was killed early in December 1931 near the Wyoming border (Young, 1946b:34). The latter individual was known in the region for the previous two years and was believed to have raised at least one litter in this period. In a report written to the U. S. Biological Survey in 1932, Louis Knowles indicated that these were the only mountain lions taken in the Hills in the previous 25 years.

The most recent specimen taken in the Black Hills to my knowledge was shot by Ted Mann on 16 December 1958 (Mann, 1959:5). He located fresh tracks in the snow on Elk Mountain, in Custer County. In the company of two neighbors and three dogs, Mann set out in pursuit of the lion, which had killed a doe and was eating on the hindquarters when the dogs jumped it. The lion, a male that weighed 140 pounds and measured about seven feet in length, finally was treed and shot along Upper Dugout Creek, about two miles south of the Stearn's Ranch.

In 1965, Fred A. Fichtner, District Ranger from Newcastle, Wyoming, reported that there had been several recent reports by ranchers of mountain lion tracks between Custer and Elk Mountain, South Dakota; "Plaster casts were made of one set, and positively identified" (letter to J. Knox Jones, Jr.). Ranger A. W. Jones, Spearfish District, noted the recent presence (1968) of a mountain lion in the vicinity of Big Crow Peak (pers. com.). Park Ranger Fred Devenport (pers. com.) indicated that two *F. concolor* were observed just inside of the west boundary of Wind Cave National Park on 10 April 1964 by Dr. Ralph Hubbard and an Indian companion, of Wounded Knee, South Dakota. Ranger-Naturalists reported seeing mountain lions in the Park on two different occasions in 1965, and on 2 April of that year, fresh lion tracks were identified in soft mud next to the pump house. A lion also was observed about this time on the ranch of Mr. Shirley McClure, southwest of Hot Springs.

Specimen examined (1).—WYOMING: *Crook County:* head Bear Creek, Bear Lodge Mountains, 1 (USNM).

Lynx canadensis canadensis Kerr

LYNX

Lynx canadensis Kerr, 1792, The animal kingdom . . ., 1:157 (type locality restricted to Province of Quebec, Canada, by Miller and Kellogg, Bull. U. S. Nat. Mus., 205: 777, 3 March 1955).

Lynx canadensis is typical of the heavily forested boreal regions of North America, but formerly occurred sparingly in suitable habitat in the Northern Great Plains region. Grinnell (1875:79) and Dodge (1876:123) both indicated that this species previously inhabited the Black Hills, and there have been several recent reports of lynx in the area. In 1944, a lynx was killed in Meade County and two more were taken in Pennington County (South Dakota Conservation Digest, 12:15, May 1945). A. H. Richardson, State Game Biologist, wrote (pers. com.) that in the last 10 years he has personally examined two specimens shot in the northern and western Black Hills.

I know of but three other individuals captured in South Dakota. A lynx was taken in Granger's Woods along the Missouri River, above Sioux City, in January 1875 (Brackett, 1881:413). A male (USNM 246548) was obtained by J. N. Martin at Bullhead, Corson County, on 6 October 1925, and another was shot by Mr. Leroy Johnson near Marindahl, Yankton County, on 6 May 1962 (Lee, 1962:21). *Lynx canadensis* presently inhabits eastern Montana (Hoffman and Pattie, 1968:53), and has been taken south of the Black Hills in the Laramie Mountains, Albany County, Wyoming (Long, 1965:708) and in northern Nebraska (Jones, 1964:304).

Lynx rufus pallescens Merriam

BOBCAT

Lynx fasciatus pallescens Merriam, 1899, N. Amer. Fauna, 16:104, 28 October (type locality, S side Mt. Adams, near Trout Lake, Skamania Co., Washington).

[*Lynx rufa*] *pallescens*—Elliott, 1901, Field Columb. Mus., Publ. 45, Zool. ser., 2:297, 6 March.

The bobcat is widely distributed in the Black Hills, being common in the foothills, in forested canyons, along wooded streams, and in areas of exposed rimrock. It remains abundant in the Hills region in spite of predator control measures. Bounties on 1311 bobcats were paid by those counties that comprise the South Dakotan portion of the Black Hills from 1962 to 1968 (records from South Dakota Dept. Game, Fish and Parks). In 30 years as a Federal Trapper, Archie Howe of Custer killed more than 450 bobcats in the Hills (Popowski, 1952:6).

Although he saw no specimens, Grinnell (1875:79) indicated that this felid was common in the Hills region. Bailey (1888:432) noted the presence of *L. rufus* near Deadwood in October 1887, and collected one individual near Custer in July 1888.

Evidently, the bobcat is an efficient predator on large game mammals. Young (1958:23) reported that "A large buck antelope was no match for a bobcat which killed it one winter day of early 1930 on the Wind Cave Game Preserve [Wind Cave National Park] in South Dakota." On 5 April 1954, George Barnes shot a 27-pound male that had just killed a yearling white-tailed buck near Wabash Spring, 5 mi N of Custer (*op. cit.*:84). However, small game also is included in the diet of this species. Stomachs of two females trapped in Wind Cave National Park by Archie Howe in early June 1924 contained only the remains of rabbits (U. S. Biological Survey files).

In January 1946, a farmer found a dead beaver, with a trap attached, floating under the ice on a stream in Palmer Gulch. He placed the carcass on the bank, set the trap, and captured three bobcats within a week (J. A. King, field notes). Stebler (1939:389) obtained a specimen of *L. rufus* along Grace Coolidge Creek in Custer State Park in August 1934. The stream was bordered with bur oak, quaking aspen, paper birch, and other deciduous trees and shrubs.

Both of the females taken in Wind Cave National Park in early June 1924 were lactating. On 17 August 1967, I shot a large female and two three-quarter grown kittens at dusk as they were leaving a den at the base of a limestone outcrop just southeast of the National Park. Thus, females of this species probably give birth to young in late March or early April in the Black Hills.

Specimens examined (38).—SOUTH DAKOTA: *Meade County:* 6 mi E Piedmont, 1 (SDSU). *Pennington County:* near Rapid City, 1 (FMNH); Spring Creek, south of Rapid City, 1 (MHM); Palmer Gulch, SE Hill City, 3 (UMMZ); 4 mi S, 14 mi W Hill City, 1; unspecified locality, 1 (NRW). *Custer County:* S Otis, 1 (UMMZ); Custer, 3 (USNM); French Creek, near Custer, 5 (USNM); Bowman Ridge, near Custer, 1 (USNM); Beaver Creek, south of Custer, 1 (USNM); Mayo, south of Custer, 1 (USNM); Streeter Ranch, 1.5 mi S, 5 mi E Wind Cave, 3550 ft, 3; Elk Mountain, 1 (USNM); Dewey, 6 (USNM).

WYOMING: *Crook County:* Otto, 1 (AMNH); Leggot Canyon, Sundance, 1 (USNM); Person Canyon, Sundance, 1 (USNM); Sand Creek Canyon, 1 (USNM). *Weston County:* Newcastle, 1 (USNM).

UNSPECIFIED LOCALITY: Black Hills, 3 (2 USNM, 1 WCNP).

Additional records (see text also).—SOUTH DAKOTA: *Custer County:* Bull Springs, 14 mi NW Custer (Lamster, 1943:1). *County unspecified:* Calumet Draw (South Dakota Conservation Digest, 17:5, June 1950).

ORDER ARTIODACTYLA—Even-toed Ungulates

Artiodactyls in the Black Hills belong to the suborder Ruminantia, and are represented by three families with five genera and six species. A seventh species, the mountain goat, was introduced from western montane areas. An additional species, the fallow deer, has been intro-

duced from the Old World, but is not well established in the Hills as yet. Four of the native species, wapiti, pronghorn, bison, and mountain sheep, previously were extirpated or drastically reduced in numbers, and subsequently have been reintroduced from other areas. Artiodactyls comprise a varied assemblage of hooved and horned, or antlered, mammals that were economically important to early explorers and pioneers. The present-day game species still provide recreation for outdoorsmen and much ecological information in the following accounts is drawn from conservation and game management literature.

Family CERVIDAE—Elk and Deer

Cervids are mainly browsers. Antlers are present at least in males and are shed annually. This family is represented in the Black Hills by two genera and three species.

Cervus canadensis canadensis Erxleben

Wapiti

[*Cervus elaphus*] *canadensis* Erxleben, 1777, Systema regni animalis . . ., p. 305 (type locality, eastern Canada, probably the vicinity of Montreal according to V. Bailey, Proc. Biol. Soc. Washington, 48:187, 15 November 1935).

The wapiti, or American elk formerly occurred throughout most of temperate North America; it has been reintroduced in many areas where it previously had been extirpated by man. The subspecies *C. c. canadensis* was native to the Black Hills, but, once it became extinct, the area was restocked with *C. c. nelsoni* from Wyoming. *Cervus canadensis* may be conspecific with the earlier-named red deer, *Cervus elaphus,* of Eurasia (McCullough, 1969), but I retain *canadensis* pending definitive study of their relationships.

The Custer Expedition of 1874 saw only a few elk, but several were killed along Boxelder Creek near Nemo on 11 August (Winchell, 1875:53; O'Hara, 1929:252). Grinnell (1875:83), who accompanied General Custer, gave the following account that partially indicated the prior abundance of wapiti in the Hills: "On Elkhorn Prairie [Reynolds Prairie] we came upon a collection of horns gathered together by the Indians. Three lodge-poles had been set up in the ground so as to form a tripod, and supported by these were a pile of [wapiti] horns 8 to 10 feet high. The horns had been shed, and had apparently been collected from the surrounding prairie [isolated prairie in the middle of the Black Hills] and heaped up here by the Indians." Dodge (1876:132), describing a hunt along the northern rim of the Black Hills, noted that a hunter "followed a large elk trail into a little valley" that was densely vegetated and that at the report of his gun, "the whole valley was alive with rushing animals; at least a hundred, crashing through the brush, disappeared up the mountain side." *Cervus canadensis* was present in the limestone country of the Black Hills, Bear Lodge Mountains, Sundance Mountains, and along Stockard Beaver and Inyankara Creeks, Weston County, Wyoming, in 1885 (Murie, 1951:42), and Bailey (1888:434) noted that some were "said to occur still" in the Black Hills in 1887.

Near the turn of the century, J. A. Allen (1895a:263) indicated that the wapiti had been extinct in the Black Hills for several years. Thus, the original population of wapiti (*C. c. canadensis*) was mostly exterminated from the Hills by 1900, and initial restocking with *C. c. nelsoni* from Wyoming commenced. About 65 were stocked at Custer State Park in 1912, but these escaped into the surrounding Hills and were replaced by an additional 25 in 1913; 50 more of these large cervids were obtained from Montana in 1916. Wind Cave National Park initiated a wapiti herd with 21 animals from Jackson Hole and Yellowstone National Park in 1914. Currently there are about 1200 wapiti in the State Park, and 450 in the National Park (Cahalane, 1948:253). The herds are controlled by driving excess animals out of the confines of the parks into the surrounding Black

Hills, or by issuing hunting permits each year.

Presently, there are two herds, totaling about 1000 elk, ranging through the Black Hills (Evans, 1966:9). A small "northern herd" traverses the limestone region along the South Dakota-Wyoming border, and a "southern herd" in habits the area adjacent to the National and State parks (A. H. Richardson, pers. com.). In the 1966-67 hunting season, 198 wapiti were killed by hunters in Custer State Park, 40 (19 bulls, 15 cows, and six calves) were taken from the "northern herd," and 40 (21 bulls, 13 cows, and six calves) were shot from the "southern herd" (Rapid City Journal, p. 9, 15 January 1967).

There is much variation in the antlers of this species in the Black Hills, and deformations are not uncommon; some antlers are much flattened near the extremities, being somewhat palmate in nature. Wapiti retire to dense forests during daylight hours, descending onto the valley meadows in early evening. Bugling of males can be heard in the autumn during mating season, and calves are born in late May or early June.

Specimens examined (4).—SOUTH DAKOTA: *Lawrence County:* 2 mi S Tinton, 6100 ft, 2. *Custer County:* 1 mi NW Wind Cave, Wind Cave National Park, 1 (WCNP). WYOMING: *Weston County:* 0.5 mi E Buckhorn, 6150 ft, 1.

Odocoileus hemionus hemionus (Rafinesque)

Mule Deer

Cervus hemionus Rafinesque, 1817, Amer. Monthly Mag., 1:436, October (type locality, mouth of the Big Sioux River, South Dakota).

Odocoileus hemionus—Merriam, 1898, Proc. Biol. Soc. Washington, 12:100, 30 April.

The mule deer, or black-tailed deer, inhabits broken country, open plains, and brush or woods of western North America. An estimated 10 million mule deer inhabited the continent when European man arrived (Merwin, 1971:33). This species occurs throughout the Black Hills but is most abundant in the ravines of foothills, and in the more remote and rugged sections. Both the mule deer and white-tailed deer were an important source of food for early travelers and settlers of the region; accounts of Hayden (1856:79; 1859:706), Grinnell (1875:84), Dodge (1876:131), Bailey (1888:434), and J. A. Allen (1895a:283) indicated that *Odocoileus hemionus* was present in the Hills in considerable numbers. However, market hunting and other factors essentially eliminated deer from most of South Dakota in the early 1900's (Seton, 1929b:332); only 225 deer, mostly *O. hemionus,* were taken legally in South Dakota in 1920 (*op. cit.*:250). A "buck law" and other legislation passed in the period between 1911 and 1925 enabled the populations of deer to increase in abundance once more by 1940 (Merwin, 1971:33). Currently, overpopulation and over-utilization of available range are the major problems in managing the ever increasing Black Hills deer herd.

The number of deer in the Hills in 1969 was estimated at 103,846—23 percent of which were *O. hemionus* (Richardson, 1969b:25; Richardson and Russel, 1970:3). Pellet group counts (based on a 365-day accumulation) conducted along 107 belt transects in 1970 indicated a 16 percent decrease in the Black Hills deer population over that of 1969. Northern Hills herd decreased 23.0 percent; central Hills herd decreased 14.6 percent, and southern Hills herd increased 5.3 percent (Thompson and Hausle, 1971:8). Mule deer are native to the Black Hills, but the species currently seems to be declining in abundance, occurring only in small pockets throughout the region, with greatest concentrations in the southern portion of the Hills. The ratio of white-tailed deer to mule deer varies from area to area. The herd in Wind Cave National Park and that of Fall River County are composed almost entirely of mule deer (F. Devenport, pers. com.), whereas in the western section of Custer County, there are equal numbers of each species. However, mule deer

predominate on the "West River Prairies" immediately adjacent to the Black Hills, with the white-tail being essentially a dweller of wooded river bottoms (Bever, 1957:4); for example, 74 percent of the 12,910 deer taken by hunters in this area in 1968 were *O. hemionus* (South Dakota Conservation Digest, 36:4, December, 1969).

Projected kill of deer in the 3517 square miles of the South Dakotan portion of the Black Hills in 1968 was 4.02 deer per square mile and was composed of 31 percent white-tail does and 45 percent white-tailed bucks, 10 percent mule does and 14 percent mule bucks (Rose 1970, Tables 4-6).

South Dakota State Game Biologist A. H. Richardson (pers. com.) suggests that one of the main reasons for the decrease of mule deer in the Hills is the preference of this species for an open, rolling type of habitat; in the past 20 to 40 years, ponderosa pine has enclosed many former environs of this type (Bever, 1959:4). In addition, white-tails seem to be the more aggressive of the two species in the Black Hills, forcing out the mule deer. Also, relative percentage of mule deer killed in the Hills by hunters is greater than that of white-tailed deer. Differential response of the two species to harsh weather conditions suggests another possible explanation of the problem. For example, from 29 April to 4 May 1953, snow in excess of 44 inches fell in the northern Hills. *Odocoileus virginianus*, in the higher portion of the Hills, migrated 10 to 25 miles down to the lower slopes and foothills during the winter for better browse and more equitable weather conditions. Mule deer did not migrate as readily, but simply shifted to more favorable exposures in nearby steep canyon drainages (Berner, 1953b:10; Harris, 1953:16; Hodgins, 1956:14).

Southwest slopes, from which the snows melt most rapidly, and tops of ridges, from which the snows are readily blown by winds, are areas on which the deer concentrate in the winter. The vicinity of Annie Creek, Lawrence County, serves as the main winter range for mule deer, whereas white-tailed deer overwinter on the Hepler Range of the northern foothills. Both species utilize the Aztec Hill, McVey Burn, Crow Peak, and Piedmont winter ranges. The critical period for deer in the Black Hills is from January to April, and many cases of death due to malnutrition in winter have been recorded (Gastler *et al.*, 1951: 356). The severe blizzard in the winter of 1948-1949 resulted in the deaths of 40 deer per square mile in the McVey Burn region (Berner, 1953a:4). Mule deer are especially susceptible to starvation and large herds in Spearfish Canyon must be fed high protein concentrate each winter due to overuse of the wintering grounds (Harris, 1952a:7), 1953:14; Brady, 1955:13; Leopold, 1956:4). Such aggregations in restricted areas further complicate the problems. A survey of browse in April and May 1969 indicated that in 2633 square miles of wintering range in the Hills, 92 square miles were over-utilized; 208 square miles were properly utilized, and 2333 square miles were under-utilized (Richardson, 1969: 3). Over-utilization occurred on the McVey Burn, Crow Peak, and Piedmont ranges, and in the area of mountain mahogany west of Custer.

Rut extends from early November to mid-December. Fawns, usually twins, are born in the Black Hills in May and June. Deer lice (*Lepoptena depressa*) parasitize deer of the Wind Cave National Park herd externally (Wind Cave National Park files).

Specimens examined (24).—SOUTH DAKOTA: *Lawrence County:* 1 mi S, 4 mi W Spearfish, 1. *Pennington County:* Rapid City, 1 (USD); Beaver Creek Valley, 4 mi N, 10.5 mi W Deerfield, 6400 ft, 1; 3 mi N, 4 mi E Hill City, 1. *Custer County:* Pleasant Valley Ranch, 6 mi SW Custer, 2 (AMNH); Campbell's Ranch, Elk Mountain, 4800 ft, 1 (USNM); Redbird Canyon, Elk Mountain, 6000 ft, 1 (USNM); Elk Mountain, 5 (USNM). *Fall River County:* 1 mi N, 4 mi E Edgemont, 2600 ft, 1.

WYOMING: *Crook County:* Bear Lodge Mountains [not 9524 (=U. S. Biological Sur-

vey skull number) feet as noted by Long, 1965:713—7242 feet is the highest elevation in the Black Hills], 2 (USNM). *Weston County:* 3 mi E Newcastle, 1; unspecified locality, 7.

Odocoileus virginianus dacotensis Goldman and Kellogg

White-tailed Deer

Odocoileus virginianus dacotensis Goldman and Kellogg, 1940, Proc. Biol. Soc. Washington, 53:82, 28 June (type locality, White Earth River, Mountrail Co., North Dakota).

Occurring throughout much of North America, white-tailed deer characteristically inhabit woodlands, forest edges, and thickets along streams. An estimated 40 million white-tailed deer inhabited the continent when European man arrived (Merwin, 1971:33). On the Great Plains, this species occupies deciduous riparian communities, but seemingly avoids extensive open areas. *Odocoileus virginianus* is numerous and widely distributed in the Black Hills, preferring timbered areas with adequate cover and water that support a good forb and browse understory. The main wintering ranges are in the foothills, and on the McVey Burn in Pennington County. This species is extremely adaptable to human populations and is quite common in agricultural areas. In 1969, there were in excess of 70,000 white-tailed deer in the Black Hills proper (Richardson, 1969b:25).

Grinnell (1875:83) wrote that this species was abundant in the vicinity of Castle Creek and the Elkhorn Prairie [Reynolds Prairie] about the head of Elk Creek, and all through the northeastern portion of the Black Hills. He noted that 100 deer, principally of this species, were killed by the command of General Custer on 9 August 1874 east of Custer Peak. Of 16 does killed by Dodge (1876:121) between 15 August and 10 September, only two had given birth to fawns that season. Approximately 1000 deer were taken by the Newton-Jenney Survey along Castle, Rapid, and Boxelder creeks (*op. cit.*:122), causing Dodge to state that *O. virginianus* was "more abundant than any other animal" in the Black Hills. In strong contrast to these reports is that of Bailey (1888:434), who wrote that "the black-tail [mule deer] is very common through the Hills but the white-tail seems to be absent. I can find no one who has ever seen this deer here." Evidently, Bailey was in error in his obserations, or confined his queries to the foothill region, because notations by W. W. Granger in 1894 agreed with the previous accounts (J. A. Allen, 1895a:263).

Odocoileus virginianus dacotensis differs from *O. v. ochroura* of western Wyoming (Long, 1965:714) and *O. v. macrourus* to the east (Kellogg, 1956: 44) in average larger size, heavier dentition, and paler color. However, there seems to be extreme variation in size within the geographic range of *O. v. dacotensis.* Evidently, white-tailed deer in the Black Hills region also are quite variable and may represent a broad zone of intergradation with the adjacent subspecies. Jones (1964:319) felt that the alleged differences between subspecies did not appear to be great. The enigma remains due to a lack of specimens for examination.

Grinnell (1875:83) indicated that the differences in size between the whitetails in the Black Hills and those on the prairie were so great that hunters of the region thought the Black Hills deer to be a different species than that to the east. Dodge (1876:130) reported: "a few days previous to the arrival of General Cook, I killed near Rapid Creek two enormous bucks, each of which, after disemboweling, and having head and legs cut off, weighed nearly one hundred and thirty pounds. In the hunt on Boxelder [with General Cook], one of the guests killed a buck just as old and just as fat as those killed by me on Rapid, but which, dressed in the same way, weighed scarcely forty pounds." Dodge indicated that both the large and small forms were found together in the same herd, as well as animals representing gradations in size between the mentioned extremes. Grinnell wrote as follows to Seton

(1929b:321): "In 1874 when with Custer's expedition to the Black Hills, L. H. North and I killed in the Black Hills three or four extraordinarily small deer." Numerous authors went on record in *Forest and Stream*, and *Recreation* magazines during the period 1895 to 1900 as having seen small white-tailed deer in the Black Hills. Measurements of a pair of diminutive white-tail antlers from Inyan Kara Mountain, found in 1890 by Robert Ansley (Seton, 1929b:316) are followed by those of a similarly-sized pair found in the Bear Lodge Mountains by Vernon Bailey in 1913 (USNM 202513): distance from burr to tip of antler, 8 inches, 10 inches; greatest distance between any two corresponding points, 10 inches, 8.5 inches; distance from base of one antler to base of second antler, 2 inches, 1.75 inches; distance from tip of one antler to tip of other antler, 8.5 inches, 4.75 inches. A few unusually small adult white-tails still are killed by hunters each season in the Black Hills (Over and Churchill, 1945: 51; Bever, 1957:4).

Nutrition may be a possible explanation of the problem. Both white-tailed deer and mule deer in the Hills are smaller in body size than are prairie representatives of the same respective subspecies (Berner, 1953c:12). Over-population and over-utilized range are characteristic of the Black Hills herd, but not of the prairie herd. Food habits are essentially the same for mule deer and white-tailed deer in the Black Hills, and have been reported by Hill and Harris (1943), Hill (1946), Gastler *et al.* (1951), Bever (1954), and Schneeweis (1968). As determined by pellet counts, deer utilize mixed aspen-pine communities to a greater extent than pure stands of either pine or aspen (Kranz and Petersen, 1970:5). Important browse species (based on observation, surveys of browse utilization, and analysis of stomach contents of 320 deer taken in the northern section of the Hills) are as follow: ground juniper, creeping juniper, quaking aspen, bur oak, ponderosa pine, paper birch, hawthorn (*Crataegus succulenta*), hop hornbeam, redroot, hazelnut (*Corylus cornuta*), Oregon grape, bearberry, wolfberry, snowberry (*Symphoricarpos canadensis*), Juneberry (*Amelancheir canadensis*), serviceberry (*A. spicata*), chokecherry, and russet buffaloberry (*Shepherdia canadensis*). Forbs utilized by the Black Hills deer include pea vine (*Lathyrus ochroleucus*), American vetch (*Vicia americana*), blue aster (*Aster laevis*), meadow sweet, wild pea (*Lupinus argenteus*), pussy toes (*Antennaria microphylla*), wintergreen (*Pyrola* sp.), alfalfa, red clover, wild rose, soapweed, and various mushrooms, grasses and lichens (*Usnea* sp.). Kentucky bluegrass comprised over 90 percent of the grasses consumed (Hill, 1946:49).

Progulski and Duerre (1964:27) found that deer in the Hills were most active between one and five hours after sunset. They indicated (*op. cit.*:31) that activity was most concentrated in lush meadows that were interspersed with brushy cover along streams. Richardson and DeMarce (1967:8) analyzed the numbers and distribution of deer in the Black Hills in 1966 and 1967, based on a 365-day accumulation of deer pellets. They found 19.7 percent of the deer occurred in the northeastern section, 47.7 percent in the northwestern-central section, 22.0 percent in the southeastern-central section, and 10.6 percent in the southeastern section of the Hills.

Mr. L. Dunn of Sturgis shot a white-tailed buck with palmated antlers near Moskee, Crook Co., Wyoming in 1965; there were 13 points on a side and the antlers much resembled those of a small moose (Lee, 1965:19). In the autumn of 1968, Dr. Calvin Schad shot a white-tailed buck in the Black Hills that had three antlers: a normal four-point antler on the left side of the skull, and two three-point antlers, arising separately, on the right side (South Dakota Conservation Digest, 36:13, April, 1969).

Rut begins early in November in the Black Hills, reaching its maximum during the latter part of the month. Does

first breed as yearlings and usually bear twin fawns from late May to early July. On one occasion I witnessed a doe with three fawns near Custer. Mule deer-white-tailed deer hybrids have been reported from the Hills but none have been authenticated (Bever, 1957:5).

During late summer and early autumn of 1952 and 1956, outbreaks of epizootic hemorrhagic disease (EHD) killed hundreds of white-tailed deer and an occasional mule deer in western South Dakota, including Meade, Pennington, Custer, and Fall River counties (Shope *et al.*, 1960; Pirtle and Layton, 1961; Trainer, 1964). Of the two viral strains known to be causative agents, the "Black Hills strain" is far less virulent than the "South Dakota strain" that causes epizootic outbreaks among prairie deer (Parikh, 1970:1). These EHD-causing strains currently are under investigation by virologists at South Dakota State University. Deaths by automobiles is another mortality factor. For example, more than 30 deer were killed on highways in the northern Hills from 16 September to 12 October 1952 (Harris, 1952c:16).

Specimens examined (29).—SOUTH DAKOTA: *Lawrence County:* 3 mi S, 3.5 mi W Spearfish, 1. *Pennington County:* 16 mi W Hill City, 6600 ft, 1; 5 mi W Hill City, 2; near Pactola, 1 (USD); 6 mi NE Keystone, 2; 4 mi N, 2 mi E Keystone, 4800 ft, 1; 20 mi N Elk Mountain, 1 (USNM). *Custer County:* Pine Creek, 1 mi N Harney Peak, 1 (SDSU); Elk Mountain, 2 (USNM).

WYOMING: *Crook County:* Bear Lodge Mountains, 13 (USNM); Lost Canyon, 5000 ft, 1 (UW); unspecified locality, 2 (AMNH). *Weston County:* unspecified locality, 1.

Additional records.—SOUTH DAKOTA: *Lawrence County:* Elk Creek (Harris, 1952b: 12). *Custer County:* Bull Springs, 14 mi NW Custer (Lamster, 1943:14). WYOMING: *Crook County:* Moskee (Lee, 1965:19). Crook's Tower (Chicago Tribune, 12 November 1941). UNSPECIFIED LOCALITY: Black Hills (Hoffman, 1877:100).

Family ANTILOCAPRIDAE—Pronghorn

The pronghorn is not an antelope but is a member of a unique family that has evolved exclusively in North America and is represented in the Black Hills region by one Recent species. Both sexes of this species possess permanent bony outgrowths from the skull that are covered with highly keratinized horny sheaths; these sheaths are shed and replaced annually. Pronghorn are grazers and inhabit the open flat country and gently rolling uplands of the Great Plains.

Antilocapra americana americana (Ord)

Pronghorn

Antilope americana Ord, 1815, *in* Guthrie, A new geographical, historical, and commercial grammar . . ., ed. 2, 2:292, 308 (type locality, unknown; noted in the original description as found "on the plains and high-lands of the Missouri").

Antilocapra americana Ord, 1818, Jour. Phys. Chim. Hist. Nat. et Arts, 87:149.

Pronghorns now are reduced in numbers over much of their former range. An estimated 30 to 40 million once roamed over the western half of the United States (Long, 1965:716). Agricultural pursuits of man and settlement of former pronghorn range contributed to a decline in the abundance of this species (Nelson, 1925:3). Hoffman (1877:100) indicated that a fatal epidemic raged among pronghorns in the summer of 1873, and that J. A. Allen estimated that from three-fourths to nine-tenths of the population may have been destroyed in some areas. Coincident with this epidemic, an epizootic disease killed most of the government stock and Indian ponies in western South Dakota. Hoffman (*loc. cit.*) noted that "If the horse epidemic was not the cause of fatality among the antelope, it is at least in very remarkable coincidence." Nearly 64 percent of the Indians at this time were affected with cerebro-spinal meningitis, and suffered a 10 to 12 percent mortality. The Indians procured their drinking water from the same pools where their ponies drank.

On 16 October 1804, Indians told Meriwether Lewis and William Clark that the pronghorn were then on their

fall migration west to the "Black Mountains" to spend the winter (Bailey, 1927: 28). Hayden (1862:150) wrote: "In the beginning of winter they [pronghorn] may be seen for days following each other in files (if not disturbed) on their way towards the Northwest, leaving the prairie for the more rugged portions of the country near the Black Hills or the foot of the mountains. In the spring, usually about March, they may be seen returning again, and distributing themselves over the open prairie." Seton (1929b:421) also reported that pronghorn of the open country flock to the Black Hills "from all points on the compass" to winter.

In his review of the status of the pronghorn, Nelson (1925:3) recorded 11 bands, totaling an estimated 680 individuals, as being resident in South Dakota, and Berner (1954:2-3, 1955:2-3) summarized the history of the pronghorn in South Dakota. At present, spring inventory of pronghorn is carried out by the South Dakota Department of Game, Fish and Parks each year. The aerial count, conducted from 3 June to 8 July 1970, indicated that the population in western South Dakota numbers about 25,000 individuals, representing a six percent increase over the 1969 estimate (West, 1971:1). A census of pronghorn in counties east of the Missouri has not been attempted for several years, but 302 individuals were killed by hunters in these areas in 1968 (West, 1970:2).

Present rangeland management in western South Dakota is oriented toward grasses and other graminoid plants. Because native woody range plants and forbs are high in fats, oils, carotenes, protein, and other constituents necessary for winter maintenance of both big game and domestic livestock, West (1971:4) suggested the need for re-establishment of these browse-plants species. The current population of pronghorn on that portion of the prairie adjacent to the Black Hills is about 82 percent of estimated carrying capacity (see Table 28).

In managing pronghorn, the Department of Game, Fish and Parks divides sections of South Dakota into "Hunting Units" that can be censused and administered independently. Units that surround the Black Hills are as follow: Unit 3, western Butte County (just north of the Hills); Unit 4, eastern Butte and northwestern Meade counties; Unit 9, southern Meade, central Pennington, and western Custer counties; Unit 14, eastern Fall River County; Unit 6, western Fall River and southwestern Custer counties. Table 28 summarizes the composition of the 1970 pronghorn populations in these respective units (see West, 1971:Tables 1 and 2).

A herd of about 300 pronghorn currently is maintained in Wind Cave National Park. Dr. W. T. Hornaday of the Bronx Zoo, and the Boone and Crockett Club, contributed the money for the initial restocking of the Park in 1914.

TABLE 28.—Estimated composition of the 1970 populations of *Antilocapra americana* in Hunting Units that border the Black Hills (West, 1971).

Hunting Unit	Number of bucks	Number of does	Number of kids	Doe:kid ratio	Population size	Carrying capacity
3	480	950	970	100:102	2400	3500
4	533	886	806	100:91	2225	3350
6	315	516	489	100:95	1320	1600
9	288	432	480	100:111	1200	1500
14	275	436	389	100:89	1100	1000
Total or average	1891	3220	3134	100:97	8245	10950

With permission of the Canadian authorities, 13 six-month-old kids were purchased from Mr. Blazier of Brooks, Alberta, for $125.00 each. These were reared for a short time, then were liberated in the Park that October (Nelson, 1925:9; Grinnell, 1929:139; Wind Cave National Park files). Disease and predators reduced the number to eight by 1915, and nine more were purchased from Alberta in 1916. Coyotes and bobcats continued to take a high toll of the pronghorn until predatory animal hunters were detached to the Park by the U. S. Biological Survey; these hunters eliminated several hundred predators (Nelson, 1925:17). By 1924, only six animals (all does) survived, but a young buck was captured near Bisner, Nevada, and released in the Park in July. The herd numbered only 28 by 1929 (Grinnell, 1929:140), but 40 individuals survived the disease and drought of the 1930's. Pronghorn finally were well-established in the Park by 1948 and numbered about 150 animals, in spite of the loss of 35 individuals to poachers in the previous year (Cahalane, 1948:256). It is probable that control of carnivores in the region no longer is of merit owing to the natural balance that now exists between predator and prey.

Management programs have involved transporting live-trapped individuals to areas of low population density for release. These introductions have been numerous and difficult to trace. Twelve kids were introduced into Custer State Park from Indian Creek Flats, Butte County, in 1916, and 10 more were added in 1919 (South Dakota Conservation Digest, 36:3, 1969). Eight pronghorns trapped in Meade County were released in Custer State Park on 4 February 1952 (Berner, 1952:8). Fifty-one pronghorn were transplanted from Custer State Park to Leola Hills, near Milbank, Grant County, in 1959 (South Dakota Conservation Highlights, 1960), and 126 were transferred from Butte County to Day and Edwards counties in 1961 (South Dakota Conservation Highlights, 1962). Numerous pronghorn were captured in northwestern South Dakota for release on the Lower Brule Indian Reservation, Lyman County, and on the Igloo Black Hills Ordnance Depot, Fall River County, in 1963 (South Dakota Conservation Highlights, 1964). One hundred and twenty pronghorn were live-trapped in Wind Cave National Park in 1963 for release on the Lower Brule Indian Reservation, on private lands in Gregory County, and for the Kansas Game and Fish Commission for release in southern Kansas (Wind Cave National Park files). These are but a few instances of artificial mixing of the herds in South Dakota.

On 2 September 1964, the "Headquarters Fire" burned approximately 4000 acres of Wind Cave National Park. The kid crop of the next year was much reduced from that of previous years. Pronghorn moved into the burned area and fed mainly upon prickly pear cactus just prior to the peak of the reproductive season. False gromwell (*Lithospermum multiflorum*) is known to inhibit ovulation in some grazing mammals, and Ranger-Naturalists at the Park speculate on the possibility that cacti, from which the spines have been burned, might have had a similar effect on the reproductive potential of pronghorn (from various reports on file at Wind Cave National Park). Breeding takes place in September and young, usually twins, are born in late May and June.

Specimens examined (10).—WYOMING: *Crook County:* Sundance, 7 (USNM). *Weston County:* 3 mi S, 1 mi E Newcastle, 1; unspecified locality, 2.

Family BOVIDAE—Bison, Sheep, and Goats

This family of large herbivores is represented in the Black Hills by three species. Two of these formerly were native to the region and have been reintroduced, one being replaced by a non-native but similar subspecies. The third representative is a non-indigenous species established by man.

Bison bison bison (Linnaeus)

BISON

Bos bison Linnaeus, 1758, Systema naturae, ed. 10, 1:72 (type locality, "Quivira," central Kansas—see Hershkovitz. Proc. Biol. Soc. Washington, 70:32, 28 June 1957).

B[ison]. bison—Jordan, 1888, Manual of the vertebrate animals . . ., ed. 5, p. 337.

The number of bison that once roamed the plains of North America has been estimated between 60 and 100 million by various authors. The bison evidently was common on the broad, undulating prairies surrounding the Black Hills in the early 1800's, but at the time of the first exploration of the region by European man, it was rare to see even an occasional wanderer. Bison had wholly disappeared east of the Missouri River prior to 1870, but great herds roamed the Coteau des Prairies west of the James River in South Dakota as late as 1866 (J. A. Allen, 1877:538). This species was decimated in the region between the Grand and Cheyenne rivers about 1869, although occasional stragglers frequented the plains toward the Black Hills until somewhat later (Hoffman, 1877:101).

When Lt. G. K. Warren (1859:630) and his command traversed the western edge of the Black Hills in September 1857, they encountered a large force of Hunkpapa and Miniconjou Sioux in the vicinity of Inyan Kara Mountain, Crook County, Wyoming. Warren gave the following account: "In the first place, they [the Indians] were encamped near large herds of buffalo, whose hair not being sufficiently grown to make robes, the Indians were, it may be said, actually herding the animals. The intention of the Indians was to retain the buffalo in their neighborhood till their skins would answer for robes, then to kill the animals by surrounding one band at a time and completely destroying each member of it." Fearing that Warren's expedition would disperse the bison, the Indians forced it to turn back southeastward. Most writers have attributed the rapid extermination of the bison over southwestern South Dakota and adjoining portions of Wyoming to white man, rather than to the Sioux Indians. If the Sioux often hunted in the manner described by Warren, then their contribution toward the decimation of bison in the Black Hills region was great indeed.

General W. F. Raynolds (1865:27), in the course of leading an expedition to explore the Yellowstone in 1859, caught first sight of the "lords of the prairie" as his command approached the Black Hills. When military posts just to the west of the Black Hills were abandoned in 1868, bison were still abundant, 50 tons being killed for garrison use in one day; yet, by 1871 no bison survived in eastern Wyoming (J. A. Allen, 1877:544). Grinnell (1875:84), while accompanying General Custer in 1874, observed no live bison in the Black Hills, but found a few skulls with the hide still attached, indicating recent presence of this bovid. Much later, Fryxell (1926:103) also discovered bison remains in the Black Hills.

Bison in the Black Hills today are the result of reintroduction. In 1913, the National Bison Society provided $26,000 with which to purchase bison to restock the Wind Cave National Game Reserve. W. T. Hornaday secured the nucleus herd of 14 animals (seven bulls and seven cows) from the Bronx Zoo through the New York Zoological Society on 28 November 1913. These bison were originally acquired by the zoo from William C. Whitney of the October Mountain Game Preserve in the Berkshire Hills near Lenox, Massachusetts, in 1903. Whitney, in turn, purchased them from H. K. Gliddon, of Moosehead Ranch at Jackson, Wyoming; one of the bulls had been captured wild in the panhandle of Texas by Colonel Charles J. "Buffalo" Jones. Two bulls and four cows from Yellowstone National Park were added to the herd in 1916.

The Custer State Park bison herd, now the second largest in the United States, was started in 1914. The South Dakota State Legislature appropriated $15,000 to stock the reserve with 36 ani-

mals (Six bulls, 18 cows, and 12 calves) that were purchased from the James "Scotty" Philip estate, Fort Pierre, South Dakota. This herd originated from five calves captured along the Grand River near Fort Bennet, in northwestern South Dakota, by Peter Dupree in 1882. The Dupree herd increased to 60 by 1900, when Philip purchased the entire stock. An additional 60 bison were obtained by the State Park from the Pine Ridge Indian Reservation, Rosebud, South Dakota, in 1951 (South Dakota Conservation Digest, 20:23, December, 1953).

Presently, approximately 350 animals range over 27,220 acres in Wind Cave National Park, and about 1550 animals range over 72,000 acres in Custer State Park. These numbers are maintained by culling and selective harvesting. For example, 276 bison were auctioned by Custer State Park in 1968 at a live sale and 138 others were butchered (South Dakota Conservation Digest, 36:29, December 1969). Each autumn, usually in October, the bison in Wind Cave National Park are rounded up by use of helicopters, horses, and vehicles, herded into a corral, branded, and treated for Bangs disease (Brucellosis). Excess animals are removed for slaughter and sale in cooperation with the State of South Dakota (South Dakota Conservation Digest, 20:3-5, 7; Griffith, 1958:16-19). In 1968, 10 hunting permits ($500 each) were issued to hunt bison in Custer State Park.

Throughout most of the year, bulls remain solitary, or in small groups. About late July, the bulls begin to join the cow-calf herd and mating occurs, usually in August. Calves are born between mid-April and June, after a gestation period of about nine months. Presently, the Wind Cave herd is being studied extensively by Milo Schulte, Iowa State University, Ames, Iowa. Garretson (1938) and Roe (1951) have written valuable accounts concerning the past history, distribution, and natural history of bison.

Specimens examined (2).—SOUTH DAKOTA: *Custer County:* "Wind Cave Game Reserve," 1 (USNM). *Fall River County:* Hot Springs, 1 (USNM).

Additional records (see text also).—SOUTH DAKOTA: *Custer County:* French Creek (Grinnell, 1875:84).

Oreamnos americanus missoulae
J. A. Allen

Mountain Goat

Oreamnos montanus missoulae J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20:20, 10 February (type locality, Missoula, Missoula Co., Montana).

Oreamnos americanus missoulae—Hollister, 1912, Proc. Biol. Soc. Washington, 25:186, 24 December.

Mountain goats are not native to the Black Hills (Swift, 1941:441) and otherwise have not become established east of the Continental Divide. In February 1924, U. S. Senator Peter Norbeck and State Game Warden L. C. Hawley obtained six goats, four females (a yearling and three adults) and two males (a yearling and an adult), from near Banff, Alberta, Canada (Gilliland, 1968a:3). These were placed in a 20-acre pen in Custer State Park, but an adult female and a yearling male escaped the first night. Warden Hawley indicated to Hanson (1950:21) that no young were born to the captive goats, but Harmon (1944:149) stated that the remaining four increased to eight by 1929, at which time all escaped (when a tree fell across the pen fence) to the rugged Elkhorn country near Harney Peak. The herd increased to 300 by 1949, and the population has remained at about that level to the present time. Goats were transplanted to Spearfish Canyon, north of Savoy, several years ago, but none has been observed there since then (South Dakota Conservation Digest, 22:11, July, 1955).

Oreamnos americanus is stenoecious in the Black Hills, inhabiting only the Mount Rushmore-Needles-Harney Peak area in the southern part of the crystalline central basin, where moss- and lichen-covered granitic ridges are thrust upward nearly perpendicular to the sur-

rounding forest. The range of this species in the Hills comprises approximately 32,000 acres, of which only 2080 acres are "primary range" (Schara, 1967:22). Population density on the primary range is about 12 goats per square mile, and approximates four goats per square mile on less desirable range (Hanson, 1950: 27).

Harmon (1944:149-151) and Hanson (1950:55-63) reported on the food habits and natural history of the Black Hills mountain goat herd. Feeding takes place at short, irregular intervals throughout the day, but most intensive foraging occurs from late afternoon to dark. Food plants generally include mosses, lichens, grasses, bracken fern (*Pteridium aquilinum*), yarrow (*Achillea lanulosa*) currant (*Ribes inebrians*), fleabane (*Erigeron* sp.), bearberry, serviceberry, chokeberry, hazelnut, buffaloberry, meadow sweet, paper birch, willows, quaking aspen, ponderosa pine, white spruce, and ground juniper. The most important food of all seasons, both in preference and in quantity consumed, is the tree lichen known as "old-man's beard" (*Usnea barbata*). Feeding sites and food habits vary with season. In spring, the goats feed on succulent graminoid vegetation in small grassy parks, near rocky areas, along the bottoms of canyons. In summer and autumn, they forage among small coves of aspen and birch scattered over slopes and ridges. In winter, the goats retire to the timber, or descend to protected areas such as the gulches of Grizzly and Pine creeks, there competing with deer and elk for available food. Winter foods consist of 60 percent mosses and lichens, 20 percent bearberry, 10 percent pine twigs and needles, and 10 percent miscellaneous browse, grasses, and weeds. Goats frequently visit salt blocks placed atop Harney Peak by the U. S. Forest Service.

In the Black Hills, district seasonal migrations are limited or nonexistent, aside from short altitudinal movements correlated with procurement of food (Bever, 1955:4). Mature goats in the Hills evidently establish individual home ranges and remain within these limits the year around (Hanson, 1950:74). Although home ranges overlap one another to varying degrees, the goats seldom gather into groups except during rut.

Mating usually occurs in October and November. After a gestation period of about 180 days, one (usually) or two (occasionally) young are born in April or May in a secluded place amid dense timber that is intermingled with rockpiles (Hanson, 1950:42). Kids are weaned the following August, but may accompany the mother until the next young is born. Reproduction does not occur until two years of age. Of 233 goats sampled from July 1948 to February 1949, Hanson (1950:28) reported 138 adults, 36 yearlings, and 59 young.

Shed of the long outercoat begins in mid-April; the worn outer fur is completely shed by early July. The shorter undercoat molts in the latter part of this period. A new outer coat is fully grown by mid-September (Hanson, 1950:36-38).

A recent survey by Arthur H. Richardson (pers. com.), State Game Biologist, indicated that the browse plants have been severely overused, with preferred food species being drastically reduced in the primary range of the goats. Trapping operations indicated that the general health of the herd was declining rapidly. In order to combat a feared population crash, the first mountain goat season was held in 1967. Forty-six goats were taken by hunters in the next two years, several of which were large enough to be registered with the Boone and Crockett Club. On 8 March 1956, a large male scoring 53¼ points, was found dead along Grizzly Creek, 3 mi E Harney Peak (South Dakota Conservation Digest, 24:5, August, 1956).

Visceral samples colected from 28 goats in the 1967 and 1968 hunting seasons revealed that the population was heavily infested with endoparasites (South Dakota Conservation Digest, 36:5, December, 1969). Three kinds of

cestodes (*Moniezia benedeni, Taenia hydatigena,* and *Thysanosoma actinoides* in the intestines) and 11 kinds of nematodes (*Protostrongylus rushi* and *P. stilesi* in the lungs; *Ostertagia circumcincta, O. ostertagi, O. trifurcata, Trichostrogylus axei,* and *T. columbriformis* in the abomasa; *Nematodirus helvetianus* and *N. maculosus* in the small intestine; *Oesophagastomum venulosum* and *Trichuris* sp. in the caeca) have been identified from these visceral samples (Boddicker and Hugghins, 1969; Boddicker, 1970; Block, 1970; Boddicker *et al.,* 1971). Ticks (*Dermacentor andersoni*) and chewing lice (*Bovicola oreamnidis*) parasitized mountain goats in the Black Hills externally (Boddicker *et al.,* 1971:95), and residues of 0.59 parts per million of chlorinated hydrocarbons (heptachlor epoxide, dieldrin, DDD, and DDE) were isolated from kidney fat of 13 goats (*op. cit.*:101).

Overcrowding of available range and heavy lungworm infestations that result in diseases of the lungworm-pneumonia complex probably are major factors in controlling population levels of mountain goats in the Black Hills. A treatise on this species and its management currently is in press (A. H. Richardson, The Rocky Mountain Goat in the Black Hills. South Dakota Dept. Game, Fish and Parks, Bull. 2, Pierre).

Specimens examined (2).—SOUTH DAKOTA: *Custer County:* Harney Peak, 1 (SDSU). *Unspecified County:* Black Hills, 1 (SDSU).

Ovis canadensis auduboni Merriam

MOUNTAIN SHEEP

Ovis canadensis auduboni Merriam, 1901, Proc. Biol. Soc. Washington, 14:31, 5 April (type locality, Upper Missouri, probably Badlands between the Cheyenne and White rivers, South Dakota).

Mountain sheep formerly inhabited foothills and prairie breaks, as well as mountainous areas, in the western United States, but now occupy only rough buttes and canyons in the more rugged mountains. *Ovis canadensis auduboni,* a subspecies that now is extinct (Cowan, 1940: 542), was native to the Black Hills. Introduction (Jackson, 1944:28) of the morphologically similar western subspecies, *O. c. canadensis,* accounts for the present occurrence of mountain sheep in the Hills.

Honess and Frost (1942:4) indicated that *O. c. auduboni* may be indistinguishable from *O. c. canadensis.* Lacking specimens, I follow Cowan (1940:542-543), who critically examined material from throughout the range of the species, in applying the name *auduboni* to the native mountain sheep of the Black Hills and adjacent areas. However, Cowan (1940:543) noted that "*O. c. auduboni* based as it is on slight cranial characters presented by a small number of specimens is to be regarded as a weak race."

In 1833, Maximillian reported that the Manitarii Indians usually went to the Black Hills and associated mountainous tracts to hunt mountain sheep, killing a hundred or more in a season (Thwaites, 1906:246). However, the maps of Maximillian labeled the Killdeer Mountains and the Badlands of the Little Missouri River (both in North Dakota) as the "Black Hills" (Bailey, 1927:25). Members of the Newton-Jenney U. S. Geological Survey shot a mountain sheep along a small tributary of Boxelder Creek on 20 July 1875 (Dodge, 1976:129). Seton (1929b:535) reported that mountain sheep were essentially gone from the Black Hills by 1887, although a few lingered on until 1899 when the last individual about which he had information was killed. W. S. Phillips, however, indicated that mountain sheep ranged in the summer of 1890 from Sundance, Wyoming, to the Inyan Kara and Bear Lodge mountains, all along the western slopes of the Black Hills (Grinnell, 1904: 334-335), and J. A. Allen (1895a:263) reported a small herd in the vicinity of Harney Peak near the turn of the century. No sheep were seen by Seton (*loc. cit.*) when he visited the Hills in the summer of 1902, but a band of about 200 *O. canadensis* still survived to the east in

the White River Badlands, near Porcupine Hill in 1909 (Charles, 1964:23). The idea that native sheep were initially prairie dwellers (Grinnell, 1928:1) and were driven to the mountains seems to be more closely associated with *auduboni* than with any of the other races (Buechner, 1960:21).

A herd of eight *Ovis canadensis*, obtained from Alberta, Canada, in 1922 by U. S. Senator Peter Norbeck, was confined in Custer State Park, but a soremouth virus all but eliminated them by 1961. A new herd was brought in from Montana about 1965 and now consists of from 50 to 70 sheep (A. H. Richardson, pers. com.). Some individuals, mainly rams, escaped into the surrounding Hills. Possibly, additional individuals from other herds introduced into nearby areas in western South Dakota may have reached the Black Hills. Twelve mountain sheep obtained from Alberta were released on the Claude Olson Ranch, Slim Buttes, Harding County, in 1961 (Nachtigal, 1961:4), and 22 from Colorado were received at the Badlands National Monument in 1963 (Charles, 1961: 5; Conservation Highlights, South Dakota Dept. Fish, Game and Parks, 1964).

In January 1967, a single ewe with one lamb was observed in the Red Valley in Wind Cave National Park. A skeleton was found in the same area in the summer of 1968, creating some doubt as to the survival of the ewe and lamb. On 15 January 1969, nine mountain sheep (one adult male, seven adult females, one juvenile male) were transplanted from Dubois, Wyoming, to the northwest side of the Inyan Kara Mountain in sec. 24, T. 49 N, R. 63 W, Crook County, Wyoming. Eight of these ascended the mountain slope, but one female escaped across the prairie. As of 8 October 1969, the mature ram and one female died; however, four new lambs have been observed (F. C. Windsor, pers. com.).

Specimens examined (1).—SOUTH DAKOTA: *Custer County:* Wind Cave National Park, 1 (WCNP).

SPECIES OF UNVERIFIED OCCURRENCE

SPECIES INCORRECTLY REPORTED FROM THE BLACK HILLS

Sorex vagrans monticola Merriam, 1890.—Baker and Findley (1953:382) reported a specimen of the vagrant shrew from 2.5 mi N Fairburn, Custer Co., South Dakota. They wrote as follows: "We have tentatively referred this specimen to S. *v. monticola* Merriam on geographic grounds, although certain cranial measurements taken show the shrew to be much smaller than other shrews of this subspecies. . . ." Subsequently these same authors (Findley and Baker, 1956: 543) assigned the same specimen to *Sorex nanus* (see account of that species). Findley (1955:26) suggests that a segment of the ancestral S. *vagrans* stock might have persisted in the Black Hills during the Sangamonian interval.

Sorex vagrans obscurus Merriam, 1891.—Long (1965:522) reported a specimen of the vagrant shrew in the Museum of Natural History, The University of Kansas, from a locality 3 mi NW Sundance, 5900 ft, Crook Co., Wyoming. There is no evidence that such a specimen ever existed at the Museum; however, there is an additional specimen of *Sorex cinereus haydeni* beyond the number indicated by Long for the specified locality. Findley (1955) revised the species *Sorex vagrans* and listed no specimens from Crook County; yet, Long (1965:520) wrote, ". . . my findings agree with his [Findley] concerning S. *vagrans* in Wyoming." Thus it appears that Long's report of the vagrant shrew occurring in the Black Hills is in error.

Myotis evotis evotis (H. Allen, 1864.) —The long-eared myotis has been reported from the Badlands to the southeast of the Black Hills and from Harding County to the north. It also is known

from much of Wyoming, excluding the northeastern portion of the state. Previous reports of *M. evotis* from the Hills were erroneous. Of three specimens listed by Stebler (1939:389) from Custer State Park, South Dakota, one is *Myotis thysanodes*, and the other two are *M. keenii*. One reported from 1.5 mi E Buckhorn, Weston Co., Wyoming (Long, 1965:532) also is *M. thysanodes*.

Geomys bursarius lutescens Merriam, 1890.—Long (1965:613) reported a specimen of the plains pocket gopher from 0.5 mi N and 1 mi E Beulah, 3550 ft, Crook Co., Wyoming, that allegedly was housed in The University of Kansas, Museum of Natural History. I have examined the museum catalogue and species card files, the field notes and catalogues of members of the field party that collected at this site, and all specimens of *Geomys bursarius* from Wyoming in the Museum's collections. Nowhere is there evidence of the indicated specimen and Long's report thus may be considered as being erroneous. Representatives of this species have been taken on the flood plains of the Cheyenne River, on the southern periphery of the Hills. There are three specimens from 1 mi E Edgemont and two specimens from 6 mi S Hot Springs (UMMZ), Fall River Co., South Dakota. D. G. Adolphson recently retrieved several skulls of this species from pellets of a barn owl nesting under the Hat Creek bridge on Highway 71, 15 mi S Hot Springs, in Fall River County (Martin, 1971a, b).

Phenacomys intermedius intermedius Merriam, 1889.—Coues and Allen (1877: 216-217) recorded a specimen of *Arvicola* (*Pedomys*) *haydeni* (USNM 3056) taken from the "Black Hills." They considered the individual as being peculiar and accredited it to being "a young of the year." Upon reexamination, J. A. Allen (1894a:331) assigned the specimen to a new species of *Phenacomys* (*P. truei*, which is in the synonymy of *P. intermedius*). In actuality, the individual was collected by W. A. Hammond on 10 August 1857 "along a wagon road to Bridger Pass" in the region now known as the Laramie Mountains, Wyoming, and the heather vole does not occur in the Black Hills.

Zapus princeps princeps J. A. Allen, 1893.—When composing the general list of mammals collected by W. W. Granger in 1894, J. A. Allen (1895a:262) included *Zapus princeps* (actually, these were *Z. hudsonius*) among those mammals taken in the Black Hills, but not from the Badlands. Yet, in the species accounts (*op. cit.*:266), the only western jumping mice obtained by Granger were listed as from Corral Draw in the Badlands. I know of no representatives of this species from western South Dakota or northeastern Wyoming, where only *Z. hudsonius* occurs.

Spermophilus lateralis lateralis (Say, 1823).—The golden-mantled ground squirrel does not inhabit the Black Hills at the present time. Coues and Allen (1877:818) listed a male of this species that was collected in the "Black Hills" on 21 July of 1859 by W. S. Wood, who accompanied the expedition of Lieutenant F. T. Bryan through the Laramie Mountains, and who, to my knowledge, did not enter the Black Hills proper. *Spermophilus lateralis* does occur about 110 miles to the southeast, in northeastern Albany County, Wyoming (Long, 1965:588).

SPECIES OF UNCERTAIN STATUS IN THE BLACK HILLS REGION

Didelphis marsupialis virginiana Kerr, 1792.—A young opossum that was captured in northern Converse County, Wyoming, by Mr. Hans W. Larsen, subsequently escaped from a cage in Newcastle, Weston County, in 1962 (Long, 1965:515). Individuals of this species have been observed in recent years in Mellette and Todd counties, South Dakota, and a specimen was captured in 1958 at Alliance, Box Butte Co., Nebraska (Jones, 1964:58). The opossum

now may be expanding its range into the Black Hills from the east by way of the deciduous riparian communities of river systems.

Sorex nanus Merriam, 1895.—The dwarf shrew has been reported just east of the Black Hills on the basis of a partially decomposed specimen recovered from a stubblefield 2.5 mi N Fairburn, Custer Co., South Dakota. The individual first was reported as *S. vagrans* (Baker and Findley, 1953:382), but later was assigned to *S. nanus* (Findley and Baker, 1956:543). The partial skull was reexamined recently by Robert S. Hoffmann and me, and we concur with the assignment of this specimen to *S. nanus*. On 3 March 1970, Don Polen, South Dakota School of Mines and Technology, captured a female of this species, along with two female *Sorex cinereus*, in a grassy field about 10 miles east of the Hills, at a place 3 mi E Boxelder, Pennington Co., South Dakota (Martin, 1971b). External measurements of this specimen were as follow: total body length, 82; tail length, 35.5; and hind foot length, 9. Martin (1971a, b) also reported a left mandible of *S. nanus* from a barn owl pellet picked up 15 mi S Hot Springs, Fall River County. Dwarf shrews usually are found in subalpine and alpine rockslides, at elevations of 8000-10,000 feet; thus, the three specimens from South Dakota are unusual both in the low altitude at which they were taken and in the habitat they occupied (Hoffmann and Taber, 1960:233).

Ecological distribution of the dwarf shrew seems to be independent of the availability of ground water. These animals seldom have been taken in snap-traps, but recent use of pitfalls has proven to be a successful method of obtaining specimens (Brown, 1967:622). Unfortunately, the majority of trapping in the Hills region has been by use of snap-traps and dry rocky areas have not been investigated thoroughly.

The ancestor of *S. nanus* "may have occurred in the Black Hills and isolated mountains of Arizona and New Mexico during the Sangamonian interval and remained in these general areas during the Wisconsin age" (Findley, 1955:28). Montane habitat in the Black Hills presumably would be suitable for the dwarf shrew and future application of pitfall sampling techniques should produce specimens from this region.

Myotis grisescens A. H. Howell, 1909. —On 21 August 1968, Mr. Tim Joseph of Menden, Missouri, captured a banded (B6-02491) male bat (presumably a *M. grisescens*) in a small cave near Savoy, Lawrence Co., South Dakota (Gunier, 1971:5). The bat previously had been captured near Tipton, Moniteau Co., Missouri, in 1967. It was transported to Higginsville, Lafayette Co., Missouri, about 65 miles northwest of the site of capture, to a place where it was released in a region where there are no known caves (Gunier, pers. com.).

The intervening distance between Higginsville and Savoy is approximately 640 linear miles across the semiarid Northern Great Plains. Presumably, this environ would be a substantial barrier to a cave-inhabiting species such as *M. grisescens*. At no previous time has this chiropteran been taken anywhere near South Dakota. The gray bat definitely is not a normal component of the Black Hills mammalian fauna and identification of bat B6-02491 and the circumstances of its recapture thus remain suspect. At best, the record represents abnormal wandering of a displaced mammal that was liberated in strange surroundings.

Euderma maculatum (J. A. Allen, 1891).—The rare spotted bat has been recorded from south-central Montana and from Big Horn County in northern Wyoming. This species possibly will be found along the deep moist canyons that are bordered by exposed limestone cliffs in the northern portion of the Black Hills.

Lepus americanus seclusus Baker and Hankins, 1950.—The snowshoe hare evidently does not occur in the Black Hills,

even though the distribution maps of Burt and Grossenheider (1964:212) and notations of Seton (1929c:739) indicate its presence there. Forest Rangers stationed at Newcastle have "heard of snowshoe rabbits" around Moskee, Crook Co., Wyoming, but I know of no specimens from the Hills. Baker and Hankins (1950:64) stated: "Immediately eastward of the Bighorns, there are no snowshoe rabbits; at least none has been reported from any of the higher areas where they might be expected to occur, as for example, the Black Hills." Montane habitats of the Hills presumably would be suitable for this species, however.

Lepus californicus melanotis Mearns, 1890.—Black-tailed jackrabbits rarely may occur on the fringes of the Black Hills. Game Warden H. J. Brockley and Forest Ranger Duke Kocer both have indicated an abundance of blacktails on the flats to the east and south of the Hills. I found one killed on a road a few miles southeast of Hot Springs, Fall River County, in June 1968. Other specimens have been reported nearby as follow: 1 mi N and 3 mi E Orin, Converse Co., Wyoming (Long, 1965:552), and 25 mi E and 20 mi S Rapid City, Custer Co., South Dakota (Findley, 1956:2). In 1956-57, fur dealers from western and southwestern South Dakota reported skins of 8500 black-tailed jackrabbits (South Dakota Conservation Digest, 24: 67, June 1957). The majority of these probably were from Nebraska and Wyoming, but there is evidence of increased numbers near the Hills.

Spermophilus spilosoma obsoletus Kennicott, 1863.—When Kennicott (1863:157-158) described *Spermophilus obsoletus*, he did not designate a holotype, but had at hand seven cotypes on which he based the description and name (Lyon and Osgood, 1909:168-169); A. H. Howell (1938-130) later selected one of these as the lectotype. Among the cotypes is a specimen, received by the Smithsonian Institution from Lieutenant G. K. Warren, that was collected by F. V. Hayden in the Black Hills of Nebraska Territory [now South Dakota] sometime in the period 1857-58. This specimen now is housed in the Museum of Comparative Zoology, Harvard University (MCZ 4817, formerly USNM 3252/4795—G. M. Allen, 1931:252), although I have not examined it.

Ground squirrels of this species prefer sandy soils having sparse or low-growing vegetation. A single specimen of *S. s. obsoletus* has been taken along the south fork of White River in southwestern South Dakota (A. H. Howell, 1938:131) and 12 others have been reported from the three southeasternmost counties in Wyoming, viz. Platte, Goshen, and Laramie (Long, 1965:577). Despite extensive collecting, no additional specimens have been obtained in the Black Hills. Several Ranger-Naturalists at Wind Cave National Park reported seeing *Spermophilus spilosoma* in the upland prairie regions of the Park in the summer of 1968. Although I suspect that their identifications were correct, I did not observe or take any specimens of this species while conducting field work within the Park.

Perognathus flavus piperi Goldman, 1917.—The silky pocket mouse has been taken in northwestern Nebraska, and at the type locality 23 mi SW Newcastle, Weston Co., Wyoming (Long, 1965: 616). Coues (1875:303) and Coues and Allen (1877:518) reported a specimen of "*Cricetodipus flavus*" (USNM 3097) from the Black Hills. I have been unable to locate this individual in order to verify the identity, but know of no other specimens of this species from the region. However, the fine sandy loam soils along the South Dakota-Wyoming border presumably would provide a suitable environment for *P. flavus*.

Reithrodontomys montanus albescens Cary, 1903.—The plains harvest mouse occurs exclusively in upland habitats, preferably on sandy soils. The mixed-grass prairie uplands of Wind Cave

National Park and some of the drier draws of the foothills would seem suitable for this species. Although no specimens have been obtained from the Black Hills proper, *R. montanus* has been taken from localities near the Hills in Harding, Meade, Lawrence, and Fall River counties, South Dakota, and in Campbell and Niobrara counties, Wyoming. For example, on 4 September 1968 I captured a female plains harvest mouse along the grassy roadside of Highway 79, 1 mi N and 5.5 mi E Hot Springs, immediately adjacent to the Black Hills.

Onychomys leucogaster arcticeps Hollister, 1914.—A male northern grasshopper mouse was obtained at Newcastle, Weston Co., Wyoming on 20 May 1894 by Vernon Bailey. Newcastle is immediately adjacent to the Black Hills and supports elements of both the Hills fauna and the plains fauna. Additional specimens have been taken in South Dakota on the periphery of the Hills at Buffalo Gap, Custer County; Spring Creek, Pennington County (MHM); 5 mi N Hermosa, Pennington County (SDMT); on the Pine Ridge Indian Reservation in nearby Shannon County; and at several localities in Harding County, north of the study area. Specimens of *Onychomys leucogaster* from the Moorcraft area, Crook Co., Wyoming (just west of the Hills) are intergrades between *O. l. arcticeps* and *O. l. missouriensis*, but are assigned to the latter subspecies (Long, 1965:638). The northern grasshopper mouse may occur in the grasslands of the Red Valley "racetrack" in the Black Hills.

Lagurus curtatus levidensis (Goldman, 1941).—The sagebrush vole occurs west and southwest of the Black Hills in Campbell, Albany, and Laramie counties, Wyoming (Long, 1965:660), northwest of the Hills in Carter and Powder River counties, Montana (Hoffmann *et al.*, 1969:592), and northeast of the Hills in Williams and Morton counties, North Dakota (Hall and Cockrum, 1953:455). The foothills and canyons of southwestern Custer County, South Dakota, and adjacent Weston County, Wyoming, are dominated by sagebrush and mountain mahogany that should provide suitable habitat for *Lagurus*. Although this microtine has not been taken there as yet, the occurrence of preferred habitat in close proximity to the present known range of the species suggests that the sagebrush vole may inhabit the southwestern edge of the Black Hills.

Vulpes velox hebes Merriam, 1902.—Of the swift fox, Grinnell (1875:80) wrote that "this pretty little fox is abundant everywhere on the plains," and Hoffman (1877:96) indicated that it was to be found in the vicinity of the Black Hills. Much reduced by hunting, trapping, and poisoning pressures, this fox presumably could still survive in the Wind Cave National Park area. The species has been reported from Harding County in South Dakota (Visher, 1914: 90), southeastern Wyoming (Long, 1965:681), and northwestern Nebraska (Cary, 1902:67).

Urocyon cinereoargenteus ocythous Bangs, 1899.—Long (1965:682) noted that the westernmost occurrence of this subspecies is represented by a large adult female from Owens, Weston Co., Wyoming (USNM 107892); however, I have not examined this specimen. Bailey (1927:166) indicated that the gray fox occurred along the northern border of the Black Hills, and an adult male was taken near Deer Ears Butte, Butte Co., South Dakota, in 1961 (Jones and Henderson, 1963:283). The "silver gray foxes" reported as being "numerous" in the Black Hills area by Dodge (1876: 123) may have belonged to this species.

Spilogale putorius interrupta (Rafinesque, 1820).—Unfortunately, there seem to be no specimens of the spotted skunk available from the Black Hills region, even though this species undoubtedly occurs there. Merritt Cary related to A. H. Howell (1906:7) that several spotted skunks were killed in the Black Hills, near Elk Mountain, Custer

County, in 1902-03. In an unpublished manuscript, Cary indicated that this species also occurred "near Newcastle" (Long, 1965:702). W. H. Over indicated in a letter to V. Schantz (1953: 125) that "I found a skull of this little mammal in a cave in the west slope of the Black Hills." E. R. Hall showed photographs of two spotted skunks, taken at the same spot in eastern Wyoming, to R. G. Van Gelder (1959:272); one displayed the pattern of *S. p. interrupta*, and the other resembled *S. p. gracilis*. Thus, these two kinds of spotted skunks may not interbreed (see also Mead, 1968:389). It is most desirable that specimens be obtained from the Black Hills in the near future in order to shed light upon this taxonomic and biological problem. Van Gelder (1959: 251) included the Black Hills within the range of *S. p. interrupta*.

Martes americana vulpina (Rafinesque, 1819).—Mr. J. Johnson captured a pine marten (USNM 249298) near Pringle, Custer Co., South Dakota on 4 January 1930. Whether this specimen represents an escaped pet or was actually indigenous to the Black Hills fauna remains uncertain. The species may have occurred in the region in the early 1800's; Hoffman (1877:96) reported seeing several specimens about 8 mi W Grand River Indian Agency, presently in Carson County, South Dakota, and martens are known from southeastern Wyoming (Long, 1965:690).

Martes pennanti pennanti (Erxleben, 1777).—The fisher has been taken in northwestern Wyoming (Long, 1965: 691), and early trappers reported seeing it frequently in the Red River Valley of North Dakota. It is possible that this species inhabited the Black Hills prior to the advent of European man in the region.

Gulo gulo luscus (Linnaeus, 1758).—The wolverine occurred occasionally in the Black Hills in the mid-nineteenth century (Baird, 1858:184; Coues, 1877: 49). The most recently recorded specimen for South Dakota is a male killed by Mr. Kenneth Long on a sheep ranch near (south of) Timber Lake, Dewey County, on 10 April 1962 (Lee, 1962:21). Wolverines also have been recorded from northwestern Wyoming (Long, 1965:698) and western Nebraska (Jones, 1964:284).

Lutra canadensis canadensis (Schreber, 1776).—The otter once inhabited at least the major river systems on the Great Plains, and Grinnell (1875:80) speculated that it occurred in the Black Hills. Hoffman (1877:96) encountered occasional skins from west of the Grand River Agency.

Dama dama (Linnaeus, 1758).—The fallow deer is a cervid that has been introduced from Europe. A herd of fallow deer range over the Annenburg Ranch west of Spearfish, in Crook County, Wyoming. A buck was shot near Hot Springs, Fall River County, in the autumn of 1955 by Hans Palmgreen, and another was killed near Piedmont in 1943 (South Dakota Conservation Digest, 25:16, July 1956). The irregularity with which these animals have been taken in the Black Hills suggests that the fallow deer has not become firmly established in the region, and that these specimens represent an occasional stray from the Annenburg Ranch.

FACTORS INFLUENCING DISTRIBUTION AND SPECIATION

MAMMALIAN DISTRIBUTIONAL PATTERNS

Because the Black Hills represent a mountainous island habitat surrounded by grass, it is difficult to satisfactorily place the Hills within previously proposed biotic distributional areas. Furthermore, the diverse topography and heterogeneous origins of the mammalian fauna in the Hills (see below) increase the difficulties. Nonetheless, the Life-

zone concept of C. H. Merriam (1899) has some merit, in a general way, when applied to the Black Hills. Because life-zones are based on temperature, the zonal boundaries correspond closely with isotherms. Kendeigh (1954) has reviewed criticisms of this concept.

Transition Life-zone.—A warmth-adapted biota occurs on the arid prairie uplands and semiarid Red Valley that surround the Black Hills, in the deciduous riparian communities that cross these grasslands, and along the basal slopes of the foothills. Steppe-associated mammals (desert cottontail, black-tailed prairie dog, olive-backed pocket mouse, hispid pocket mouse, Ord's kangaroo rat, prairie vole, black-footed ferret, pronghorn, and bison) and riparian-associated mammals (eastern cottontail, fox squirrel, and white-footed mouse) are fairly limited to the Transition Life-zone in the Black Hills region.

Canadian Life-zone.—A cold-adapted biota occupies the forested upper slopes of the foothills and the "boreal-cap" (Limestone Plateau, Central Basin, and Bear Lodge Mountains) of the Black Hills. Several boreal or montane "isolates" are more or less restricted to this life-zone (e.g., red squirrel, northern flying squirrel, yellow-bellied marmot, red-backed vole, and to an unknown extent, the ermine). Other species, such as the least chipmunk, northern pocket gopher, and long-tailed weasel have endemic subspecies in the Canadian Life-zone of the Black Hills, whereas the Transition Life-zone is inhabited by a different subspecies or represents a broad zone of intergradation between races. Some kinds of mammals (the masked shrew, Nuttall's cottontail, bushy-tailed woodrat, long-tailed vole, and meadow jumping mouse) are far more abundant on the "boreal-cap," than in the Transition Life-zone, where they are represented by much lower population densities. Many species of mammals are not confined to either life-zone, but abide in suitable habitats in each (the white-tailed jackrabbit, thirteen-lined ground squirrel, deer mouse, and meadow vole) or range freely throughout both (large and mobile ungulates and carnivores, volant bats, and semiaquatic furbearers).

Long (1965:726-729) described several faunal areas in Wyoming, based on patterns of geographic distribution of mammals. In his system, the biota of the Black Hills is associated with the so-called Great Plains Faunal Area. Its divisions of immediate interest here are briefly discussed below.

The broad arid region that isolates the Black Hills from other forested mountains in northern and central Wyoming comprises the Powder River Valley-Bighorn Basin Faunal Division. The long-tailed vole and Nuttal's cottontail range westward out of the Hills, along streamside environs in this region. The Cheyenne Plains Faunal Division isolates the Hills from the Laramie Mountains and other southern mountain ranges in Wyoming. A small tract of this unit is in contact with the extreme southwestern corner of the Black Hills, projecting between the previous and following faunal divisions, and supporting typical plains species. The substrate of the Sand Hills Faunal Division is composed of sands or fine sandy loams that extend westward from the Sand Hills of Nebraska, along the South Dakota-Wyoming border (Sand Hill Regosol Soil Subassociation), and is inhabited by various heteromyids and other arenicolous mammals.

The Black Hills Faunal Division is delineated by the forested portion of the Hills and is inhabited by many mammals of boreal or montane affinities. The first three faunal divisions, and the lower tracts of the fourth, are assignable to the Transition Life-zone, whereas most of the fourth faunal division is applicable to the Canadian Life-zone; representative distributions of mammals in these life-zones were enumerated above.

ORIGIN OF THE RECENT MAMMALIAN FAUNA OF THE BLACK HILLS

The present biogeographic analysis of the Black Hills mammalian fauna is based on the distributions of 59 indigenous species. These include four species (the wapiti, pronghorn, bison, and mountain sheep) that previously were extirpated and then reintroduced by man, and one (the fox squirrel) that undoubtedly was introduced but probably also reached the Black Hills along natural routes of dispersal. In addition, 11 species of uncertain status are incorporated as a component of the Black Hills fauna; these species either were reported from the Hills in early literature, or specimens have been recently acquired immediately adjacent to the Hills (Table 29). Three species (the Norway

TABLE 29.—Mammals of the Black Hills, listed by faunal units as discussed in the text. An asterisk denotes species of uncertain status that probably occur (or once did occur) in the Black Hills region.

Widespread Species (26)
- *Myotis leibii*
- *Myotis lucifugus*
- *Lasionycteris noctivagans*
- *Eptesicus fuscus*
- *Lasiurus cinereus*
- *Castor canadensis*
- *Peromyscus maniculatus*
- *Ondatra zibethicus*
- *Erethizon dorsatum*
- *Canis latrans*
- *Canis lupus*
- *Vulpes vulpes*
- *Ursus americanus*
- *Ursus arctos*
- *Procyon lotor*
- *Mustela frenata*
- *Mustela vison*
- *Taxidea taxus*
- *Mephitis mephitis*
- *Felis concolor*
- *Lynx rufus*
- *Cervus canadensis*
- *Odocoileus hemionus*
- *Odocoileus virginianus*
- *Antilocapra americana*
- *Bison bison*

Steppe Species (10)
- *Lepus townsendii*
- *Spermophilus tridecemlineatus*
- *Cynomys ludovicianus*
- *Perognathus fasciatus*
- *Perognathus hispidus*
- **Reithrodontomys montanus*
- *Microtus ochrogaster*
- **Vulpes velox*
- *Mustela nigripes*
- **Spilogale putorius* (subspecies *interrupta*)

Great Basin Species (1)
- *Eutamias minimus* (karyotype B)

Sonoran Species (7)
- *Myotis thysanodes*
- *Sylvilagus audubonii*
- **Lepus californicus*
- **Spermophilus spilosoma*
- *Dipodomys ordii*
- *Reithrodontomys megalotis*
- **Onychomys leucogaster*

Deciduous Forest Species (6)
- *Myotis keenii*
- *Lasiurus borealis*
- *Sylvilagus floridanus*
- *Sciurus niger*
- *Peromyscus leucopus*
- **Urocyon cinereoargenteus*

Boreomontane Species (10)
- *Sorex cinereus*
- *Tamiasciurus hudsonicus*
- *Glaucomys sabrinus*
- *Clethrionomys gapperi*
- *Microtus pennsylvanicus*
- *Zapus hudsonius*
- **Martes americana*
- *Mustela erminea*
- **Gulo gulo*
- *Lynx canadensis*

Cordilleran Species (10)
- **Sorex nanus*
- **Myotis evotis*
- *Myotis volans*
- *Plecotus townsendii*
- *Sylvilagus nuttallii*
- *Marmota flaviventris*
- *Thomomys talpoides*
- *Neotoma cinerea*
- *Microtus longicaudus*
- *Ovis canadensis*

rat, house mouse, and mountain goat) that were introduced from outside of the study area are not treated in this analysis.

Hoffmann and Jones (1970) recently presented a comprehensive biogeographic analysis of the Recent mammalian fauna of the Northern Great Plains. Because this thorough study encompasses the Black Hills region, much of the following account is based on the substance of their report. I also have drawn from my own summary of the vegetation and affinities of the Black Hills flora (see pages 26 to 38 and Table 2).

Steppe Species.—Ten species (14.3%) of the Black Hills mammals have evolved in response to the semiarid to arid environment of the interior North American grasslands and are closely allied with the Great Plains biota. The distributions of *Lepus townsendii* (listed with both the Great Basin and Campestrian faunal units by Armstrong, 1971), *Spermophilus tridecemlineatus, Cynomys ludovicianus, Perognathus fasciatus, Microtus ochrogaster, Vulpes velox* and *Mustela nigripes* broadly overlap the Black Hills region, whereas distributions of *Perognathus hispidus* and *Reithrodontomys montanus* approach their northwesternmost limits in the Hills area, and *Spilogale putorius* (subspecies *interrupta*) reaches its westernmost limit. The latter may be distinct from the Great Basin race, *S. p. gracilis*, at the specific level (Van Gelder, 1959:272; Mead, 1968:389). Two additional kinds (*Antilocapra americana* and *Bison bison*) are intimately associated with the prairie grasslands but range beyond the central steppes and are treated with other eurytopic species. Likewise, *Lepus californicus, Reithrodontomys megalotis,* and *Onychomys leucogaster* are steppe-associated mammals but have a much more extensive distribution in the Southwest and adjacent Mexico.

During the maximal Wisconsin glaciation, much of the Northern Great Plains was covered by a boreal forest and members of the current plains biota occupied steppe or savanna conditions to the south. Pollen profiles and the presence of relict populations of *Microtus ochrogaster* (*M. ludovicianus* in western Louisiana and eastern Texas) and *Cynomys ludovicianus* (*C. mexicanus* in northern Mexico) are evidence of the southerly displacement of the Great Plains biota to suitable refugia in the Full-glacial period (Hoffmann and Jones, 1970:366). Although some restricted grassland may have occurred in the arid rain shadow of the Rocky Mountains in Late-glacial times, it was not until a shift in atmospheric circulation and ensuing climatic events occurred, in the Pre-Boreal and Boreal periods, that actual replacement of the boreal forest by grassland commenced on the Plains. Concomitantly, steppe-associated mammals dispersed northward, south of the ice front, and reinhabited the Northern Great Plains and Black Hills region.

As the plains climate became increasingly warmer and drier, conditions favored eastward extension of the grasslands biota. Guilday *et al.* (1964) recorded two prairie species, *Spermophilus tridecemlineatus* and *Pedioecetes phasianellus* (the sharp-tailed grouse), in eastern Pennsylvania in the Late-glacial period. Mid-post-glacial time also is the only period that *Spilogale putorius interrupta* ranged east of the Mississippi River, into western Illinois (Parmalee and Hoffmeister, 1957). Shifts in the plains biota presumably occurred many times and to varying degrees, but most recent authors favor the Atlantic period as the time of maximal eastward penetration of the grassland biota. In the Sub-Boreal period, the steppes retreated to their present limits.

Differential tolerance to high temperatures and accompanying heat stress may have dictated the post-glacial movements of some members of the plains biota. For example, *Microtus ochrogaster* is much more tolerant of xeric conditions than is its boreomontane congener, *M. pennsylvanicus;* yet, populations of *M.*

ochrogaster have decreased drastically in recent droughts (Wooster, 1935, 1939; Gier, 1967). The easternmost margins of the plains-grasslands presumably would be somewhat more mesic, and the eastward shift in *M. ochrogaster* during drier post-glacial times may have been in response to decreased evaporative stress in such areas. Conversely, the occurrence of *Perognathus hispidus* in eastern Missouri in Late-glacial or early Holocene time (Oesch, 1967) may be credited to the ability of this heteromyid to tolerate extremely cold temperatures (Jones, 1964:173). As a final example of temperature-influenced shifts in distribution, the present northward retreat of *Lepus townsendii* from the southern part of its range and its current expansion to the north and northeast may be correlated with the gradual warming trend now in progress on the North American continent (*op. cit.*:113).

Other factors influencing past distributions of steppe mammals include the presence of effective barriers to dispersal and the availability of food sources. The Missouri River limited the eastward expansion of *P. hispidus* and *Reithrodontomys montanus*. Past and present ranges of *Mustela nigripes* correspond closely to those of *Cynomys ludovicianus*. There are some exceptions to the last mentioned example. For instance, *M. nigripes* is represented in late Pleistocene deposits in Jaguar Cave in Idaho, and in Orr Cave in Montana, but remains of *Cynomys* apparently were not present in either deposit (Guilday and Adam, 1967:30).

Sonoran Species.—Seven kinds of mammals (10.0%) present in the Black Hills are typical of the Chihuahuan-Sonoran Region of southwestern United States and adjacent Mexican Plateau. Like the steppe species, these mammals evidently originated under the dictate of an arid climatic regime, and subsequently invaded the Hills region in times of post-glacial warmth and dryness, probably in the late Boreal and early Atlantic periods. Most of these species are associated with the interior grasslands but have extensive distributions beyond the central steppes. *Lepus californicus*, *Dipodomys ordii*, *Reithrodontomys megalotis* and *Onychomys leucogaster* also range into the Great Basin, as does *Myotis thysanodes*. The ranges of *Sylvilagus audubonii* and *Spermophilus spilosoma* are more widespread west of the Black Hills, but rarely exceed 40° latitude in the far west. *Lepus californicus*, *R. megalotis*, and *O. leucogaster* also are apportioned far east of the Hills, as was *S. audubonii* during chronic droughts of a few decades ago (Hoffmann and Jones, 1970:382).

Both *L. californicus* and *S. spilosoma* approximate their northernmost limits on the Great Plains along the southeastern margin of the Black Hills. The former species has extended northward into South Dakota within historic time, whereas the latter has not been taken in the Hills since the period of 1857-58.

Myotis thysanodes is represented by an endemic population in the Black Hills region (subspecies *pahasapensis*). Either a few individuals managed to cross intervening barriers to initiate a disjunct colony, or the population in the Hills is a relict that resulted from the fragmentation of a formerly more widespread distribution.

Great Basin Species.—Although many members of other faunal units range into the Great Basin (Armstrong, 1971, listed *Myotis volans*, *Lepus townsendii*, *Thomomys talpoides* and *Antilocapra americana* as components of this faunal unit), only one species (1.4%) of the Black Hills mammalian fauna presumably originated there. Hoffmann and Jones (1970:383-385) proposed a Great Basin-Great Plains pattern of differentiation for *Eutamias minimus*, and indicated that subspeciation of *Thomomys talpoides* and *Spilogale putorius* also may fit this general pattern. Definitive evidence concerning differentiation of the latter two species is lacking as yet.

Recent analysis of chromosomal structure of *Eutamias minimus* (Sutton

and Nadler, 1969:526) indicates that boreal forest races (*borealis* and *neglectus*), Rocky Mountain subspecies (*arizonensis* and *consobrinus*), the Laramie Mountains race (*operarius*), and two secondarily steppe-adapted subspecies (*minimus* of the Wyoming Basin and *caryi* of the San Luis Valley) possess karyotype "A." The Great Basin races (*scrutator* and *pictus*), Northern Great Plains subspecies (*pallidus* and *cacodemus*), and two montane populations (*confinis* in the Bighorn Mountains and *silvaticus* in the Black Hills) possess karyotype "B." The absence of heteromorphic chromosomes is evidence that subspecies with these two different karyotypes may in fact represent sibling species (Sutton and Nadler, 1969).

During maximal glaciation, the ancestral stock of the Great Plains races of *Eutamias minimus* evidently became disjunct from typical boreal representatives. Isolated by a barrier of coniferous forest that intervened between the Great Basin and Wyoming Basin, the ancestral stock evolved in response to arid steppe and semidesert environs that were associated with sagebrush-grass communities, as well as coniferous woodlands. The interposing coniferous forest barrier presumably was intermittent, and formed in response to climatic conditions that favored each continental and Cordilleran glaciation; thus, it was fashioned by either southerly displacement of boreal forests or by descent of montane forest. For example, regional montane biotic zones throughout the cordillera were depressed vertically 4000-4500 feet, concurrent with a decrease of 16-17°F in summer temperature in the Full-glacial period (Richmond, 1965:228, and others). A similar descent of the lower treeline evidently occurred in the Sub-Boreal and possibly other periods.

As the boreal forest retreated northward and the montane woodland ascended upslope, a relatively low nonforested pass opened across the Continental Divide between the Great Basin and Wyoming Basin. Thus the climate of the early Holocene, or possibly of prior interglacial periods, permitted movement of *Eutamias minimus* across the Wyoming Basin, onto the Northern Great Plains. A shift of the upper-air anticyclonic eddy northeastward from the Great Basin in the Sub-Atlantic period (Bryson and Wendland, 1967) may have influenced dispersal of the biota at a later time. The boreal forest chipmunks previously in the plains region, theoretically retreated upslope into montane environments, coincident with retreat of boreal elements from the prairie. Apparently freed from intense competition, the invaders from the Great Basin then adapted to the central steppes environment.

That *Eutamias minimus confinis* and *E. m. silvaticus* appear to have been derived from adjacent plains populations rather than from boreal forest or Rocky Mountain ancestors is indicative of several periods of isolation as described above. Otherwise, the montane derivatives of the plains populations would have met extremely intense competition from residual boreal chipmunks, already occupying the Bighorn Mountains and Black Hills. Probably, boreal-adapted races would have a competitive advantage in a montane environment over those that were steppe-adapted. Under what conditions steppe-adapted races would find these montane areas free of boreal-adapted chipmunks, or would become competitively superior to the latter, remains problematical.

Deciduous Forest Species.—Six species (8.6%) of the Black Hills mammalian fauna have affinities with eastern hardwood forests, mesic grasslands, or prairie riparian communities. Most of these mammals reach the westernmost limits of their continuous range in the vicinity of the Hills.

Myotis keenii (subspecies *septentrionalis*) and *Sciurus niger* are restricted to temperate eastern North America, whereas *Lasiurus borealis* (a seasonal migrant in the Hills region), *Sylvilagus floridanus, Peromyscus leucopus* and

Urocyon cinereoargenteus are widely distributed in the temperate eastern and subtropical southern portions of the continent. The last mentioned species originated in the Neotropical Region, but invaded the Northern Great Plains from the east (Hoffmann and Jones, 1970: 377). Whether *Myotis keenii* is an actual "relict" or a seasonal migrant to the Black Hills is still in question. *Peromyscus leucopus* presently occurs on the Northern Great Plains in scattered localities that are relatively isolated from their respective contiguous ranges (see Figs. 15 and 16, Hoffmann and Jones, 1970:388). The currently disjunct populations of *P. leucopus* may represent isolated segments of a formerly more or less continuous and interbreeding population that dispersed northwestward behind the retreating ice sheet and was subsequently extirpated in the more xeric climatic regimes. Alternatively, they may typify the disruption of a continuous dendritic distribution that paralleled mesic drainage systems westward across the prairies. The latter explanation is favored by most recent authors. Currently, gene-flow between these limited populations is reduced or absent, and each presumably is adapting independently to its immediate environmental conditions, as evidenced by the relatively small and dark mice on the Black Hills.

Elements of the eastern deciduous forest replaced boreal forest species along the eastern periphery of the Northern Great Plains in Pre-Boreal times. Members of this faunal unit presumably then dispersed westward along wooded tributaries of the Missouri River system, only to be excluded from the plains (or isolated in suitable refugia) in the subsequent arid Atlantic time. With amelioration of climatic conditions in the more mesic Sub-Atlantic and Neo-Atlantic periods, eastern species could disperse westward along gallery forests once more. Several species (*Sciurus niger* and *Urocyon cinereoargenteus*) have extended their ranges westward to the Black Hills area within historic time.

Widespread Species.—Twenty-six species (37.1%) of the Black Hills mammals are eurytopic, with no apparent faunal affinities in relation to the Hills region. These kinds are present in the study area because they typically are extremely mobile. They are euryecious with a wide range of tolerance for various environmental factors, or are stenoecious but encounter specific environmental requisites in several segregated habitats throughout the region.

Volant bats, and large ungulates and carnivores, are exceedingly mobile, ranging over vast areas that may be composed of several different environs. Of the eurytopic chiropteran fauna, *Myotis leibii* is restricted to temperate North America, whereas *M. lucifugus* and *Lasionycteris noctivagans* also range over boreal portions of the continent, and *Eptesicus fuscus* and *Lariurus cinereus* additionally are distributed to the Neotropical Region. Two of these species (*L. noctivagans* and *L. cinereus*) are seasonal migrants in the Black Hills.

Of the large game mammals and furbearers whose distributions overlap the Black Hills, five are primarily temperate kinds (*Taxidea taxus, Lynx rufus, Odocoileus hemionus, Antilocapra americana* and *Bison bison*), three are mainly temperate-boreal taxa (*Vulpes vulpes, Mephitis mephitis* and *Cervus canadensis*), three are temperate-boreal-subtropical types (*Canis lupus, Ursus americanus,* and *U. arctos*) and five species (*Canis latrans, Procyon lotor, Mustela frenata, Felis concolor,* and *Odocoileus virginiana*) range from temperate regions into both boreal and Neotropical areas. Three of these mammals (*U. americanus, P. lotor,* and *O. virginiana*) are primarily associated with woodlands throughout their ranges, whereas four others (*T. taxus, O. hemionus, A. americana,* and *B. bison*) are associated for the most part with nonforested environs. The remaining nine species occur in both major habitats.

Three stenoecious aquatic or semi-

aquatic mammals are included in the eurytopic faunal unit, *Castor canadensis*, *Ondatra zibethicus*, and *Mustela vison*. These are temperate-boreal species with specialized niche requirements that are fulfilled by a variety of aquatic habitats throughout their range.

Among widespread terrestrial rodents, *Erethizon dorsatum* is a temperate-boreal species that usually is associated with coniferous trees, but has an extensive distribution beyond such forests. *Peromyscus maniculatus* best exemplifies a euryecious taxon. This species consists of a long series of interbreeding, or potentially interbreeding, populations distributed from northern boreal North America southward to Oaxaca, Mexico. It is ubiquitous, occupying a remarkable variety of habitats and, being quite responsive to local environmental selective pressures, has formed numerous ecotypes throughout its range.

Boreomontane Species.—Ten species (14.3%) of the mammals inhabiting the Black Hills are distributed both in the northern boreal forest and in the coniferous forest of western montane areas. Mammals of the boreomontane faunal unit for the most part range much farther north than do members of the cordilleran faunal unit; southern limits of distribution also average farther north for the former than for the latter.

Boreal forest, displaced southward by continental glaciation, and montane forest, displaced downslope, eastward and southward by Cordilleran glaciation, probably intermixed along a broad front, maintaining a continuous coniferous woodland throughout the Powder River Valley and Cheyenne River plains. The boreomontane biota in the Black Hills was thereby connected with that of the Bighorn and Laramie mountains until at least the Pre-Boreal period. Several forested corridors that provided avenues for dispersal of boreomontane mammals remained on escarpments and other topographic breaks well after the coniferous forest retreated upslope and northward (Hoffmann and Jones, 1970: 386 and Fig. 1).

Relict populations of northern mammals that now are disjunct from other such populations, and from the main range of the species, are an indication of the widespread extirpation of boreal elements during the Atlantic period and other warm, dry climatic episodes. Only the hardiest colonies survived the xeric conditions, and these abided in the favorable or tolerable cool and mesic pockets on the plains, or in montane regions.

Three boreomontane mammals (*Sorex cinereus*, *Microtus pennsylvanicus* and *Zapus hudsonius*) are widely distributed across the Northern Great Plains in suitable riparian communities. The latter species lacks a western montane distribution typical of other members of this faunal unit, and often occurs in populations that are isolated from others by broad expanses of inhospitable terrain.

A few species (*Martes americana*, *Gulo gulo* and *Lynx canadensis*) represent northern kinds that presumably inhabited the Black Hills in the recent past, but have since become extinct there. Occasionally, some representatives of these species may still wander into the Hills region.

The remaining four species (*Tamiasciurus hudsonicus*, *Glaucomys sabrinus*, *Clethrionomys gapperi*, and *Mustela erminea*) represent "glacial relicts" that probably were isolated subsequent to the northerly retreat of the ice sheet. *Mustela erminea* is disjunct in the Black Hills to an unknown extent; it is present in the Laramie Mountains, but apparently absent in the Bighorn Mountains. The level of divergence of *Clethrionomys gapperi brevicaudus* (previously regarded as a distinct species) suggests that this vole may have become disjunct earlier than did other "isolates," or may have diverged at a faster rate; the opposite supposition may apply to *Glaucomys sabrinus* and *M. erminea* (see the following section on Speciation). Cockrum and Fitch (1952) indicated that

C. g. brevicaudus is closely related to *C. g. galei*, and thus may have cordilleran-montane affinities. However, until more evidence is available, my comments here are based on the more northern distribution of the species as a unit.

The subspecies of *T. hudsonicus* in the Black Hills (*dakotensis*) appears to be more closely related to the reddish-colored boreal forest populations than to the darker-colored Rocky Mountain races (Hoffmann and Jones, 1970:372). Reddish-colored squirrels in the northern Laramie Mountains, southeastern Montana, northwestern South Dakota, and other outlying areas probably are remnants of the former population that remain distributed along past corridors and dispersal routes. Assuming that *dakotensis* originated in response to selective pressures of the Black Hills environment, the race either enjoyed a broader distribution in early Holocene time, or has since dispersed outward from the Hills via pine-filled canyon systems and conifer-dominated escarpments.

Cordilleran Species.—Ten species (14.3%) of the Black Hills mammalian fauna represent elements that were displaced into the region by Cordilleran ice sheets. These mammals evidently became stranded after retreating upslope in response to increasing aridity in postglacial time. All but three species attain their easternmost limits on the Northern Great Plains in the Black Hills—the range of *Neotoma cinerea* and *Ovis canadensis* extend slightly beyond, terminating in western South Dakota, and *Thomomys talpoides* is broadly distributed eastward to approximately 98° longitude. The plains and montane races of the latter species may have a pattern of differentiation similar to that of *Eutamias minimus*.

Myotis evotis, M. volans, Plecotus townsendii, Neotoma cinerea and *Ovis canadensis* generally are associated with montane forests, rocky outcrops, or badlands topography in western North America, whereas *Sorex nanus* usually is associated with subalpine or alpine rock slides in the central-western United States. *Sylvilagus nuttallii* and *Microtus longicaudus* have relatively broad niches, dispersing westward across the Powder River Valley plains in association with riparian communities. Of the cordilleran faunal unit, only *Marmota flaviventris* represents a distinctly disjunct population. Isolation of this marmot in the Black Hills presumably occurred in the manner assumed for other "glacial relicts."

Several taxa present in the Bighorn and Laramie mountains either failed to disperse to the Black Hills, or were extirpated there during xeric climatic regimes (Hoffmann and Jones, 1970:376 and Table 2). This fact, in conjunction with the presence of other taxa in the Bighorn Mountains that are absent in the Laramie Mountains, and vice versa, suggests a filtering effect of past barriers, or differential survival of species reaching these montane environments, or both.

Using the distribution maps of Long (1965), the number of subspecies of mammals in each of the three indicated montane environs was ascertained. Twenty-five taxa occur in all three ranges, and 19 kinds are common to the Black Hills and Laramie Mountains, but do not abide in the Bighorns. Four subspecies are shared by the Black Hills and Bighorn Mountains, but not by the Laramie Mountains. Eleven races are common to the Bighorn and Laramie mountains, but do not occur in the Black Hills. Sixteen kinds inhabit the Black Hills, but are absent from the other two ranges. Eleven subspecies occur in the Bighorn Mountains, but not in the Black Hills or Laramie Mountains, and 13 subspecies live in the Laramie Mountains, but not in the Black Hills or Bighorns. Three species (*Eutamias minimus, Marmota flaviventris,* and *Thomomys talpoides*) have diversified into separate subspecies in each of the aforementioned mountainous regions.

Employing these data, a percentage index of faunal resemblance (Simpson, 1943) can be calculated for each pair

of montane areas. Such indices are not absolute, but are meaningful only when comparing neighboring faunas, thereby yielding a relative measure of similarity (Udvardy, 1969:273). The larger the percentage index, the more closely the faunal pairs resemble each other. Computed indices between the various pairs are as follow: Black Hills and Bighorn Mountains, 56.9; Black Hills and Laramie Mountains, 68.7; Bighorn and Laramie mountains, 70.6.

Biogeographic analysis of affinities of the mammals in the Bighorn and Laramie mountains were undertaken in a manner similar to that used in the analysis of the Black Hills biota. Percentages of the mammalian fauna attributable to the respective faunal units are given for the Black Hills, followed sequentially by that of the Bighorn Mountains and Laramie Mountains as follow: widespread species, 37.1, 41.2, 36.8; steppe species, 14.3, 9.8, 11.8; Great Basin species, 1.4, 2.0, 2.9; Sonoran species, 10.0, 7.8, 8.8; deciduous forest species, 8.6, 0.0, 4.4; boreomontane species, 14.3, 13.7, 11.8; cordilleran species, 14.3, 25.5, 23.5.

Indices of faunal resemblance and biogeographic analyses both suggest that coniferous forest corridors between the Bighorn Mountains and Black Hills were indirect—via the northern Laramie ranges (Casper and Haystacks), the Hartville Uplift, and the Pine Ridge escarpment (Hoffmann and Jones, 1970: 386). This would account for the greater faunal similarities between the Bighorn and Laramie mountains, and between the Laramie Mountains and Black Hills. The relatively high percentage of cordilleran mammals in the two former montane environs, as compared to the Hills, further implies that the indirect connection was of greater duration, or was a much better dispersal route, or both, than was a direct extension of coniferous forest eastward from the Bighorn Mountains to the Hills.

Whereas the mammalian faunas of the Bighorn and Laramie mountains are similar due to a predominance of cordilleran kinds, the Laramie Mountains fauna resembles that of the Black Hills due to a greater presence of steppe, Sonoran, and eastern species. The Black Hills and Bighorn Mountains, on the other hand, both exceed the Laramie Mountains in relative proportions of boreomontane and widespread mammals. The latter mountainous region is intermediate in elevation (and perhaps other environmental factors) as compared to the former two montane areas. Another possible avenue of exchange between the Black Hills and Bighorn Mountains may have occurred to the north, via the wooded Rosebud-Tongue river breaks and conifer-clad Long Pine Hills of southeastern Montana and northwestern South Dakota.

SPECIATION AND GEOGRAPHIC VARIATION

Biotically-induced Selection Pressures.—Two pairs of related species (*Myotis evotis* and *M. thysanodes; Sylvilagus floridanus* and *S. nuttallii*) are parapatric in the Black Hills region. Several other pairs of species (*Sorex cinereus* and *S. nanus; Sylvilagus audubonii* and *S. floridanus; Reithrodontomys megalotis* and *R. montanus; Peromyscus leucopus* and *P. maniculatus; Microtus longicaudus* and *M. pennsylvanicus; M. ochrogaster* and *M. pennsylvanicus; Mustela erminea* and *M. frenata; Odocoileus hemionus* and *O. virginiana*) are known to be sympatric, but ecologically distinct to varying or unknown degrees. Specific distinctness of such species pairs strongly suggests extrinsic isolation in the past and subsequent development of intrinsic isolating mechanisms in response to differential selection pressures. Indeed, with the exception of the eurytopic deer, each member of the aforementioned species pairs belongs to a separate faunal unit of different biogeographic affinity (see Table 29). Interaction among closely related species favors differential exploitation of similar niches, thereby de-

creasing the intensity of interspecific competition.

Seemingly, selection pressures would be less stringent on those species that do not compete with congeners in the study area. However, interspecific and ecological interactions between various sympatric genera (*Lepus* and *Sylvilagus; Eutamias* and *Spermophilus; Glaucomys, Sciurus* and *Tamiasciurus; Clethrionomys* and *Microtus*), among various chiropterans, and among several heteromyids may favor partitioning of similar niches in the Hills region due to these biotically-induced selection pressures.

Environmentally-induced Selection Pressures.—Many kinds of mammals have differentiated into more or less distinct subspecies as the result of selection pressures engendered by the Black Hills environment. Four of these subspecies (*Myotis thysanodes pahasapensis, Tamiasciurus hudsonicus dacotensis, Marmota flaviventris dacota,* and *Clethrionomys gapperi brevicaudus*) currently are disjunct and continue to adapt independently. Three others (*Eutamias minimus silvaticus, Thomomys talpoides nebulosus* and *Mustela frenata alleni*) are represented on the surrounding plains by different subspecies (*E. m. pallidus, T. t. bullatus* and *T. t. pierreicolus, M. f. longicauda* and *M. f. nevadensis*), and are presumed to be in genetic contact with these surrounding populations. The presence of parapatric subspecies implies either that the two races formerly were isolated and diverged (but not to the extent of developing intrinsic isolating mechanisms) in response to different environments before subsequent contact with the step cline, or that subspecific divergence occurred *in situ* due to strong selective pressures that formed separate clinally connected ecotypes. The extreme contrast between the Black Hills and Great Plains in climate, topography, and biotic communities enhances the feasibility of the latter mechanism. The general pattern of variation in other mammalian species (see following discussion) also suggests *in situ* divergence of clinally connected ecotypes in the Black Hills region.

For the most part, the Black Hills are inhabited by races of mammals that also inhabit the encompassing plains. Continual exchange of hereditary materials between the Hills and plains populations seems probable. Dichromatism (dark and pale phenotypes) and extreme individual variation in the Black Hills populations of *Peromyscus maniculatus* (Osgood, 1909:78; Dice, 1942:1-10), and of *Spermophilus tridecemlineatus* and *Microtus longicaudus* (Long, 1965:738) presumably are due to disruption of the strong selection for darker coloration in the humid Hills by influx of alleles from paler forms on the arid plains.

An additional source of variability in mammals within the Hills is due to the great diversity in physiognomy, exposure of soils, and other general edaphic characteristics. Because small mammals are intimately associated with their habitats, selection pressures in one area may be quite different from those in another.

For example, the relatively dry, hardwood-dominated drainage system of Big Spearfish Canyon and similar streambeds in the Bear Lodge Mountains contrast sharply with the cool, mesic Little Spearfish Canyon that is characterized by luxuriant moist meadows and spruce-bordered streams. As indicated in Figure 12, the general climatic regime of the northern Hills differs from that of the southern Hills. Additionally, the climatic and environmental gradations from relatively mesic higher elevations, to semiarid foothills, to arid plains is much more gradual in the southern Hills as compared to the abrupt changes typical of the northern Hills (see page 112). The occurrence of *Eutamias minimus pallidus*, rather than *E. m. silvaticus* in the extreme southern and southeastern Black Hills probably is a reflection of the gradual gradation of environmental factors, hence, of environmentally-induced selection pressures. Other small mammals in

the southern portion of the Black Hills generally tend to be slightly paler than those of the northern area. In addition, the dorsal pelage of several mammals in the northwestern sections reflect red hues more intensely than those from other areas. Species that vary noticeably within the Black Hills include *Eutamias minimus, Tamiasciurus hudsonicus, Thomomys talpoides, Peromyscus maniculatus, Neotoma cinerea* and *Microtus pennsylvanicus.*

The major effect of selection in the Black Hills as a unit seems to be in accord with Gloger's Rule, producing relatively dark and reddish-colored populations. The positive correlation indicated by Stebler (1939) and Dice (1942) between the color of dorsal pelage of mammals and the color of exposed soils in the Black Hills and on the Great Plains already has been discussed (see page 99). Dice (1947:19), after undertaking several experiments that established significant selection by barn owls for deer mice contrasting in coloration with their background, concluded that ". . . natural selection can theoretically produce rapid evolution whenever a genetically variable population is exposed to its action." Populations presumably respond to different environments through variation in gene frequencies, but natural selection tends to minimize variability, increasing the frequency of adaptive phenotypes and thus creating local ecotypes.

Clark (1938) indicated that the pale ochraceous-buff color of deer mice on the plains is a character dominant over the recessive darker coloration that frequently occurs in deer mice inhabiting montane areas. Seemingly, the environment in the Black Hills favors a higher frequency of recessive dark alleles, but the gene pool is disrupted by the influx of dominant pale alleles from the surrounding plains populations, resulting in dichromatism within Hills populations. If a similar genetic scheme may be assumed for the several isolated mammals in the Black Hills region, then genetic drift may also play a role in increasing recessive homozygosity, thereby enhancing differentiation of these disjunct populations.

The broad arid regions (Belle Fourche, Cheyenne, and Powder river plains) that isolate the Hills from other montane areas are inadequate barriers to some species. These rivers provide routes of immigration and emigration for *Sorex cinereus, Sylvilagus floridanus* (to the north, south and east), *Sylvilagus nuttallii* (to the west), *Sciurus niger, Thomomys talpoides, Peromyscus leucopus, Microtus longicaudus, Microtus pennsylvanicus, Zapus hudsonius,* and various semiaquatic mammals. Thus, genetic flow is probable along streams in these species, between riparian-restricted plains populations and those on the Black Hills. Long (1965:733) noted that among lagomorphs, the species most dependent on riparian habitats is darkest in color—*Sylvilagus floridanus* (dark), *S. nuttallii* (intermediate), and *S. audubonii* (pale).

The degree of differentiation of disjunct species in the Black Hills may be used as an indirect measure of the duration of such isolation. Such indications are relative and may be modified greatly by unknown differential rates of evolution of the species in question. For example, *Clethrionomys gapperi brevicaudus* differs from *C. g. galei* of the Rocky Mountains in 11 mensural parameters (see also Cockrum and Fitch, 1952) and previously was treated as a distinct species (Bailey, 1897:129). The remaining subspecific isolates (*Myotis thysanodes, Tamiasciurus hudsonicus,* and *Marmota flaviventris*) differ from the nearest conspecific populations mainly in color, or differ in mensural characters to a comparatively lesser extent than encountered between the two subspecies of *Clethrionomys gapperi. Myotis keenii, Glaucomys sabrinus,* and *Peromyscus leucopus* also are isolated to differing degrees and currently appear to be diverging under the dictate of natural selection in the Black Hills. The Hills

population of *Mustela erminea* appears disjunct, but evidently does not differ notably from members of this species in the Laramie Mountains. Hence, *C. gapperi* either became isolated in the Black Hills at an earlier time than did the other "glacial relicts," or has diverged at a faster rate due to a shorter generation time. Conversely, those species that have differentiated in the Hills region to a lesser extent either were isolated in a later time period or have responded more slowly to selection pressure incurred by the Black Hills environment.

Many kinds of mammals with broad distributions that overlap the Black Hills have not diverged subspecifically, but display some modification in coloration within the Hills. Populations of *Spermophilus tridecemlineatus, Neotoma cinerea, Peromyscus maniculatus, Microtus longicaudus, Microtus pennsylvanicus* and *Microtus ochrogaster* all seem to be evolving darker color in the study area. On the other hand, representatives of *Reithrodontomys megalotis* that occur in the Hills show no appreciable change in coloration when compared to those of the surrounding plains. Finally, three species (*Sorex cinereus, Peromyscus maniculatus,* and *Zapus hudsonicus*) vary clinally in coloration, and in external and cranial dimensions northwestwardly across the Great Plains (Dice, 1941:16; Robertson, 1971). With exception of somewhat darker color, the Black Hills apparently do not interrupt the clinal nature of variation in these species.

SUMMARY

The Black Hills of western South Dakota and northeastern Wyoming constitute an elliptically-shaped, isolated mountainous region of approximately 4000 square miles that resulted from intermittent domal uplifts in Cretaceous, Miocene, and Pleistocene times. Entirely surrounded by the non-glaciated Missouri Plateau section of the Northern Great Plains physiographic province, the Hills rise above the plains about 4000 feet on the east and some 3000 feet on the west; the highest point is 7242 feet above sea level. Most of the area lies within the drainages of the Cheyenne and Belle Fourche rivers. As here considered, the Black Hills are delimited by the distribution of Jurassic shale and sandstone of the Sundance Formation. The region thus circumscribed includes the Black Hills proper, as well as the Bear Lodge Mountains and Devils Tower of Wyoming; these tracts are closely allied geographically, geologically, climatically, physiognomically, and biologically. Ranges of mountains nearest to the Black Hills are the Laramie Mountains (to 10,272 ft) and Big Horn Mountains (to 13,165 ft), approximately 150 miles to the southwest and west, respectively, in Wyoming.

This report delimits and describes the Black Hills as a natural zoogeographic unit, considers the autecology and general distribution of each mammalian species in the Hills, discusses the geographic variation and inferred speciation of these mammals, and analyzes and interprets the probable biogeographic affinities of various species in light of conjectured changes in late Pleistocene and Holocene environments. Six orders and 19 families, including 44 genera and 62 species, comprise the Black Hills mammalian fauna.

Biogeographical analysis of the Recent mammalian species of the Black Hills suggests the following faunal affinities: 37.1 percent widespread, 14.3 percent steppe, 14.3 percent boreomontane, 14.3 percent cordilleran, 10.0 percent Sonoran, 8.6 percent deciduous forest, and 1.4 percent Great Basin. Indices of faunal resemblance and biogeographic analyses suggest that coniferous forest corridors between the Bighorn Mountains and Black Hills in the Pleistocene

time were indirect; this accounts for the faunal similarities between the Bighorn and Laramie mountains, and between the Laramie Mountains and Black Hills. The relatively high percentage of cordilleran mammals in the two montane environs, as compared to the Hills, further implies that the indirect connection was of greater duration, or was a much better dispersal route (or both) than was a direct extension of coniferous forest eastward from the Bighorn Mountains to the Hills.

Interaction among closely related species favors differential exploitation of similar niches, thereby decreasing the intensity of interspecific competition. Ten pairs of related species in the Hills region either are parapatric or sympatric but ecologically distinct to varying degrees. Specific distinctness of such species pairs strongly suggests extrinsic isolation in the past and subsequent development of intrinsic isolated mechanisms in response to differential selection pressures. Intergeneric competition also may favor partitioning of similar niches due to these biotically-induced selection pressures.

Four endemic subspecies currently are disjunct from contiguous populations, whereas three others are in genetic contact with different subspecies on the surrounding plains. Such parapatric subspecies probably diverged *in situ* due to local selection pressures that formed separate, clinally-connected ecotypes.

Most races in the Hills also inhabit the plains. Dichromatism in several species is due to disruption of selection for darker coloration in the humid Hills by influx of pale alleles from arid plains populations. Small mammals in the southern Hills tend to be slightly paler than those in the northwestern Hills, which reflect red hues more intensely than individuals from other areas.

Many eurytopic mammals have not diverged subspecifically in the Hills, but display modification in coloration; one species shows no apparent change. Three species vary clinally northwestwardly across the plains; the Black Hills do not interrupt these clines.

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